Community assembly in marine macrofauna communities

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AUTHOR STATEMENT

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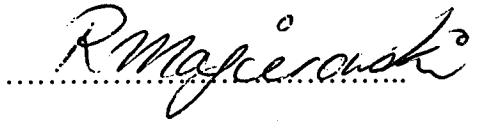

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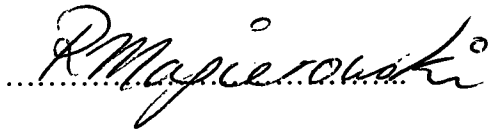

ABSTRACT

A key question in community ecology is whether communities are a natural level of biological organisation, with characteristic emergent properties influenced by evolution and comprising species that have mutually influenced each others evolution, or whether they are simply haphazard collections of species adapted to similar physical conditions. Are they a real biological phenomenon or merely artificial constructs to help biologists order their thinking? If communities are real entities determined and constrained by evolution and with distinct emergent properties, then one place to look for evidence of this is during the assembly process. A community that displays a broadly consistent structure regardless of the order of arrival and abundance of taxa and thus whose structure reflects predictable post-settlement processes and not merely the accumulation of settlers, is likely to be a real community rather than a haphazard assemblage.

Community assembly in macrofauna communities developed in artificial kelp holdfasts was monitored at 1-month intervals over a 13 month period using a sampling design that used systematic patterns of temporal overlap and changes in start and collection dates. The aim of this experiment was to study the links between recruitment and community dynamics through the assembly process by comparing community trajectories for substrata deployed on different dates, and thus subject to different potential recruitment from the larval pool. The rate of settlement is thought to be an important determinant of marine community dynamics. The design is unique in its intensity of sampling and level of replication, which could only be achieved through the use of artificial habitats.

The hierarchical nature of the experimental design allowed several different approaches to analysis; by date of deployment and by date of collection of the artificial habitats, which enabled comparison of community assembly with and without the seasonal effects of the date of collection, and by community age to test whether there were alternative end-states to assembly depending on season or recruitment history.

While the process of assembly varied across the different deployment and collection dates, community structures defining the completion of assembly, were broadly similar. This was because the interactions between individuals (interspecific and/or intraspecific) were an important structuring force. This was particularly the case in older communities, and thus, the rate of supply of recruits (relative to the frequency and intensity of disturbance) can be a key determinant of community dynamics in macrofauna communities. Richness was lower than expected from accumulation of monthly recruits, suggesting the importance of pre- and/or post-settlement competitive and/or predatory interactions. However, results were taxon specific, with evidence of settlement-driven population dynamics (*e.g.* hiatellid bivalves), facilitation (*e.g.* serpulid polychaetes) and competition/predation (*e.g.* phyllodocid polychaetes), among the 100 families examined. The behaviours of a series of null models, which displayed increasing levels of ecological realism and which were based on observed data, showed that while the interactions among individuals already established in the community influenced community dispersion, the interactions occurring between settling individuals and the established community had the greatest influence on community structure. Results on a subset of taxa of sufficient abundance for further analysis suggested that the direction of these

interactions was consistent across communities of different age. These results have implications for the way we approach the study of macrofauna communities, because recruitment to bare space is likely to be a poor indicator of the actual recruitment of organisms to an established community.

The overall results suggest that the collection of organisms that establish within an artificial kelp holdfast are more than just assemblages of settling organisms, rather they should be considered real communities. This was evident in an analysis designed to identify and assess the performance of surrogates employed to monitor community structure through changes in season and community age. While surrogate performance varied depending on the surrogate examined, with careful selection, effective surrogates of community structure could be identified. Notably, good surrogates could be identified from as few as 10% of the total number of families, but surrogates based on familial diversity within abundant higher taxa did not perform any better than random selections of the same number of families.

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1 GENERAL INTRODUCTION

1.1 Introduction

The key question of whether communities are a natural and functional level of biological organisation, rather than artificial constructs to help biologists order their thinking, is almost as old as the study of ecology itself (Drake 1990). While William Paley's view was that nature is inherently functional, within its different levels of organisation (*e.g.* individuals, populations, *etc.*), Charles Darwin argued that all of nature could be understood as the manifestation of individuals locked in a struggle for survival (Dawkins 1986, Wilson 1997). If communities are functionally organised units of biological organisation, they will have characteristic emergent properties that can be influenced by evolution (Wilson 1997), and be comprised of species that have mutually influenced each other's evolution. The alternative is that communities are merely haphazard collections of species that happen to arrive in the same place and are adapted to similar physical conditions or have similar resource requirements (Connor and Simberloff 1979, Underwood 1986). The distinction is important because how we study and manage these communities and harness them for industrial applications, and the way they respond to pressures such as global warming, the invasion of exotic species, and other major anthropogenic forcings will depend on how they are organised (Simberloff 2004).

Ecologists have debated this question in a number of different ways. Several elements of the broad question have been addressed: (1) are community dynamics deterministic (*e.g.* Clements 1916) or stochastic (*e.g.* Gleason 1926)?; (2) are assembly trajectories convergent or divergent (*e.g.* Samuels and Drake 1997)?; (3) do communities converge to a single stable equilibrium, multiple

stable equilibria or are they non-equilibrial (*e.g.* Drake 1990, Drake et al. 1993, Grover and Lawton 1993, Chase 2003)?; (4) is local richness determined solely by regional richness or do species interactions influence observed patterns of local richness (*e.g.* Terborgh and Faaborg 1980, Zobel 1997, Srivastava 1999, Russell et al. 2006)?; (5) are communities more influenced by neutral processes such as stochasticity and genetic drift than by the interactions that occur among component species (Bell 2000, 2001, Ulrich 2004, Bell 2005)?; and, (6) in marine communities, is the supply of recruits (*e.g.* Keough 1984, Gaines and Roughgarden 1985, Booth and Brosnan 1995, Caley et al. 1996) more important than the species interactions that occur pre- and/or post-settlement (*e.g.* Connell 1961, Underwood et al. 1983, Edgar 1993)? Most of these questions relate to the process of succession or assembly in a community, which is apposite since the nature of a community and its dynamics cannot be fully understood without examining the processes that influence assembly (Drake 1990, Samuels and Drake 1997, Cadotte et al. 2005).

The different questions are linked because determinism in community dynamics may be characterized by the convergence of community assembly trajectories, although this may not necessarily result in a stable equilibrium (Grover and Lawton 1993, Samuels and Drake 1997), and history (*e.g.* initial conditions) may influence whether all trajectories converge to a single or a multiple set of basic community structures (Drake 1990). One mechanism for the convergence of trajectories of different instances of particular community types, is that, as a community develops, the relative importance of species interactions (interspecific and/or intraspecific) in determining community structure increases relative to the supply of new individuals. Thus, a community that displays a

broadly consistent assembly process regardless of the order of the arrival and abundance of taxa, is likely to be a real community rather than a haphazard assemblage (Underwood 1986).

1.2 Community dynamics in marine communities

In marine communities, the question of whether supply is more important than interactions among individuals in determining community or population structures has been given much consideration (*e.g.* Keough 1984, Gaines and Roughgarden 1985, Minchinton and Scheibling 1991, Connolly and Roughgarden 1999b, Connolly et al. 2001). Since marine systems are generally more open than terrestrial and freshwater systems, the supply of individuals is likely to be an important aspect of their dynamics (Underwood and Keough 2001), both for the supply of initial inhabitants (Woodin 1991) and for the maintenance of community structure (Diaz-Castaneda 2000). Most studies have indicated that, as the rate of recruitment increases, recruitment becomes less important and interactions between individuals become more important as key determinants of community structure. This is suggested to indicate that, as free space becomes limited, the inevitable result is that individuals are more likely to interact with each other (Dayton 1971). This hypothesis is sometimes termed the recruit-adult hypothesis (Menge 2000).

Most of the work supporting the recruit-adult hypothesis in the marine environment has been conducted on sessile communities. It is not known whether the same processes are more generally applicable to other communities, including other marine communities (Menge and Branch 2001). In communities dominated by mobile species, processes influencing community dynamics may

be different to those operating in sessile communities because the supply of individuals includes adults (through migration) as well as juveniles (Frid 1989), and because individuals can move within and between communities to avoid predation and competition. In addition, the sessile communities studied to date in this context tend to be relatively species-poor compared with other types of marine communities, and it is not known whether the same results would be obtained with species-rich communities with a more complex set of interspecific interactions. This problem is also true of experimental studies examining most of the other questions outlined above. Because of the complexity of community dynamics and the problems and ethical issues surrounding large-scale experimental manipulations of species rich communities (Pimm 1991, Cadotte et al. 2005), experimentation is largely limited to species-poor communities, whether they are model systems, natural systems or lab- or field-based microcosms.

Because of their inherent complexity, species-rich communities are more often studied using an observational approach rather than a manipulative experimental approach. While phenomenological studies are important (Underwood et al. 2000), they are limited because these studies can only show the net result of the contrasting processes (both past and present) that act to influence a community's structure, and because it is difficult to avoid confounding the different mechanisms contributing to observed patterns. For example, Diamond (1975) suggested that checker-board or negative species co-occurrence patterns may be used to indicate the importance of competition in determining community structure, and Gotelli and McCabe (2002) subsequently demonstrated that non-random patterns of negative co-occurrence do indeed occur in nature. However,

several other mechanisms can also account for this pattern of species' distribution, such as founder effects (Grover 1994, Belyea and Lancaster 1999), the influence of the assembly history (Drake 1990 and Cracraft 1988 in Ulrich 2004), habitat heterogeneity (Schoener and Adler 1991), and neutral processes (Ulrich 2004, Bell 2005). In these circumstances, where it is difficult to isolate several confounding factors, it is difficult to define a null hypothesis (Pimm 1991).

1.3 Kelp holdfasts as model communities

This divide in approach to community-level analysis, where experiments are focused on species-poor communities and species-rich communities are studied using observations, demands that experiments be conducted on species rich communities that can be easily manipulated. Kelp holdfast communities are small in physical dimension, discrete and abundant throughout the temperate regions of the world, and despite the high level of species richness, they can be relatively consistent in community structure across large spatial scales (Anderson et al. 2005a, b). Thus, these communities are likely to be excellent models (Smith 2000, Anderson et al. 2005b) for experimentally examining community processes such as assembly in a species-rich community. This type of community may help to bridge results from studies utilizing microcosms, which in most cases are likely to be too simplistic to compare meaningfully to natural communities (Underwood et al. 1983, Keddy 1989), mathematical models and purely observational studies conducted at a large scale on species-rich communities. The organisms found in kelp holdfast communities are diverse in form and life history characteristics (Moore 1972, Ojeda and Santelices 1984, Smith et al. 1996), they are often rich at all levels of taxonomic resolution (*e.g.* Anderson et al. 2005b), contain both

sessile and mobile species and often provide habitat for both juveniles and adults. In this study, 100 different families were identified (Appendix 1) and individuals ranged in length from 1-50 mm. Many aspects of the structure and variability of these communities have been examined, including spatial and temporal variability (*e.g.* Ojeda and Santelices 1984, Moore 1986, Gee and Warwick 1996, Anderson et al. 2005a, Anderson et al. 2005b, Rule and Smith 2005), community assembly and/or turnover (*e.g.* Arntz and Rumohr 1982, Dean and Connell 1987a, Costello and Myers 1996, Somaschini et al. 1997, Diaz-Castaneda 2000, Norderhaug et al. 2002, Jorgenson and Christie 2003, Thiel 2003, Waage-Nielsen et al. 2003), the influence of habitat and/or habitat structure (*e.g.* Moore 1972, 1974, Myers and Southgate 1980, Smith 1996b, Smith et al. 1996, Aikins and Kikuchi 2001, Goodsell and Connell 2002, Kelaher 2002, Edgar and Klumpp 2003, Goodsell et al. 2004), resource availability (*e.g.* Edgar 1999) and the response of these communities to environmental impact (*e.g.* Jones 1972, Smith 1994, 1996a, 2000). However, little is known about the underlying processes that structure these communities (Underwood and Chapman 2006).

1.4 Thesis outline

My overall aim in this study was to examine the links between recruitment and community dynamics through the assembly process of kelp holdfast communities, by comparing community trajectories for substrata deployed on different dates, and thus subject to different potential recruitment from the larval pool. The term 'assembly' is used to describe this process rather than 'succession' because it is possible that community development may proceed in a manner other than that described by traditional models of succession (Connell and Slayter 1977), *e.g.* where early colonisers are not replaced by later

colonisers. Specifically, the aims were to contrast the relative importance of the various processes involved in assembly, and to determine whether there was a broadly consistent assembly process that might indicate that these communities are more than just a collection of organisms with similar habitat and/or resource requirements. To be certain of community age and the timing of deployment of virgin habitats, artificial holdfasts were constructed that were similar in size and dimension to the most common species of kelp found in southern Australia, *Ecklonia radiata* (C. Agardh) J. Agardh. The approach to analysis was to use both multivariate and univariate indices of community structure, because detection of community pattern may be dependent on the selection of index (Samuels and Drake 1997, Benedetti-Cecchi *et al.* 2000).

Assembly was monitored in artificial kelp holdfasts at monthly intervals over a period of 13 months using systematic patterns of temporal overlap and change in deployment and collections dates, for brevity this design is described as 'temporally hierarchical' throughout the thesis. Disturbance was rare, but when occasionally holdfasts were buried in sediment, they were removed from the analysis.

In Chapter 2, the overall assembly process in these communities is described. The hierarchical nature of the experimental design allowed for several different approaches to analysis; *viz.* by date-of-deployment and by date-of-collection of the artificial habitats, which enabled comparison of community assembly with and without the seasonal effects of the date of collection, and by community age, which enabled testing whether there were alternative end-states to assembly depending on season or recruitment history.

Results presented in Chapter 2 suggest that these communities do organise to a broadly similar community structure despite a strongly seasonal signal in recruitment. This suggests that interactions between individuals are an important structuring force in these communities. If this is true then it is likely that the recruit-adult hypothesis, developed from studies of sessile communities, also holds in communities dominated by mobile species. In Chapter 3, I examine whether there is evidence to suggest that the recruit-adult hypothesis holds for assembly in kelp holdfast communities. However, the approach differs from that typically employed to examine this hypothesis in sessile communities. In previous studies, the relative influence of recruitment and species interactions was examined by comparing population or community dynamics among sites with varying settler abundance (*e.g.* Gaines and Roughgarden 1985, Menge 1991, 2000, Connolly et al. 2001). In this study, the relative importance of these two classes of process are contrasted by examining the influence of recruitment in communities of different age and in communities influenced by different rates of recruitment. Based on the recruit-adult hypothesis, recruitment should have a greater influence on community structure in younger communities than in older ones, and for a given community age, during times of low rather than high rates of recruitment.

In Chapter 4, I extend my analysis of the relative importance of recruitment over species interactions by attempting to identify the broad types of biological interaction occurring within a kelp holdfast community and their relative influence on community structure. A series of null models based on monthly recruitment, but with increasing levels of ecological realism, were used to

generate assembly trajectories. The assembly trajectories of these predicted communities are compared to the assembly trajectories of communities established in the field. The major types of interaction examined are interactions occurring between potential recruits and the established community (recruit-adult interactions) and interactions occurring among established members of the community (adult-adult interactions). I also examine whether these interactions are negative (competitive or predatory) or positive (*e.g.* facilitation) and attempt to identify how consistent they are in interaction strength and direction across communities of different age.

The overall results of Chapters 2-4 suggest that the collection of organisms that establish within a kelp holdfast are more than just assemblages of settling organisms, rather they should be considered real communities. This has implications for the search for surrogates of community structure. Surrogates are unlikely to be consistent across temporal and spatial scales if the system under examination is an assemblage rather than a real community. In Chapter 5, I identify and assess the performance of surrogates to monitor community structure through changes in season and community age. Surrogates of community structure may provide information about a community without the time-consuming, labour-intensive and skilled task of identifying all species (Daily and Ehrlich 1995, Kitching et al. 2001).

In the General Discussion (Chapter 6), I contrast the assembly process observed in this study to existing models of succession, including models based on sessile marine communities, and conclude that these communities have characteristics consistent with predictions of what real communities should look like. I argue

that it is important to identify whether communities are a natural and emergent level of biological organisation, because this should influence how manipulative experiments are conducted.

The reader should note that the main chapters (Chapters 2-5) have been written as manuscripts for publication and consequently some level of repetition, particularly in the methods sections, was unavoidable.

2 COMMUNITY ASSEMBLY IN MARINE MACROFAUNA COMMUNITIES USING ARTIFICIAL SUBSTRATA: THE IMPORTANCE OF SEASON AND HISTORY

2.1 Abstract

The aim of this study was to examine the influence of timing of initiation (season of deployment) and recruitment history on macrofauna communities occupying artificial kelp holdfasts. This is because history (for example the order of colonisation) and season can have large effects on the assembly process and on the mechanisms underpinning a community's ongoing dynamics. We monitored assembly at monthly intervals over a period of 13 months using a temporally hierarchical sampling design. This enabled comparison of community trajectories for substrata deployed on different dates, and thus subject to different settlement signals, which provided insight into the effect of deployment history on the success of recruits and development of the community. Predictably, the season of the deployment date was an important determinant of community structure in young communities, and communities establishing from recruitment in warmer months accumulated richness and total abundance more quickly than those establishing in cooler months. However, communities ≥5 months old were broadly similar, independent of the season of deployment. This showed that communities develop towards a similar endpoint, although at a finer scale of resolution, some variability in this assembly endpoint could be explained by the season of collection. History was important because some of the variation in the endpoint to assembly was unexplained by season. Results suggest that, with careful consideration of timing of deployment and collection, artificial habitats can be a useful alternative to naturally occurring holdfasts in the monitoring of macrofauna communities for the investigation of general principles in community ecology and environmental impact.

2.2 Introduction

It is well established that history (for example, the order of colonisation) and season can have large effects on the process of assembly in a community (Drake 1990). Such effects may not only influence the trajectory observed in the community, but may also affect the mechanisms underpinning its ongoing community dynamics (Drake 1991, Cadotte et al. 2005). For example, the order of colonisation may lead to different interaction intransitivities (*e.g.* Buss 1980, McCune and Allen 1985, Drake 1991). Scale is also an important consideration in assessing the dynamics of ecological systems because the processes influencing dynamics act at different scales, and because the nature of patterns reflecting these processes depends on the scale of observation (Levin 1992, Habeeb et al. 2005). There are several examples of the use of spatially hierarchical sampling to provide information on variability in the processes determining community structure and dynamics at different spatial scales (Dunstan and Johnson 1998, Menconi et al. 1999, Anderson et al. 2005a, Anderson et al. 2005b). However, very few studies have explored the influence of the temporal scale of sampling on community dynamics (*e.g.* Atilla and Fleeger 2000, Underwood and Chapman 2006).

Temporally hierarchical designs can assist in identifying appropriate scales of sampling, and can also provide information on how assembly can vary with season, recruitment and disturbance history. This is important because most benthic systems are a mosaic of patches reflecting different intensities, frequencies and timing of disturbances, and settlement and post-settlement interactions. Thus, any field-based measurements assessing spatial variability are

inevitably confounded with temporal variability. For this reason, time is a fundamental consideration in the design of any ecological experiment, yet so often the temporal aspects of experiments are ignored for statistical convenience or, at best, are poorly explained.

In marine communities, the timing of disturbance can affect community assembly and community structure (Dayton et al. 1984, Chapman and Johnson 1990, Underwood and Anderson 1994, Nandakumar 1996) because variation in recruitment success can lead to profound differences in the dynamics of adult populations (*e.g.* Osman and Whitlatch 1996, Diaz-Castaneda 2000, Menge 2000, Connolly et al. 2001). Recruitment success will vary temporally depending on species-specific seasonality in reproductive output (Underwood and Keough 2001), temporal variation in positive ecological associations (Dunstan and Johnson 2005), predation, competition (Osman and Whitlatch 1996) and physical conditions (*e.g.* Dean and Connell 1987c, Navarrete et al. 2005), and with temporal variation in community level parameters such as richness, stability (Dunstan and Johnson 2004, 2005), dominance (Smith et al. 2004) and assembly history (*e.g.* Jenkins and Buikema Jr. 1998).

We monitored assembly in macrofauna communities established in artificial kelp holdfasts using a temporally hierarchical sampling design. We used artificial substrata because it would be impractical to apply this experimental design using natural kelp holdfasts. Our aim was to examine the influence of timing of initiation (season of deployment) and recruitment history on these communities. Macrofauna communities in kelp holdfasts and on artificial substrata have both been identified as useful model communities to investigate environmental impact

(*e.g.* Jones 1972, Smith 2000, Anderson et al. 2005b), but information on their temporal consistency is required if they are to be used for this purpose (Moore 1986, Smith and Rule 2002, Anderson et al. 2005b, Rule and Smith 2005). The experimental design enabled comparison of trajectories of community assembly for substrata deployed on different dates. The temporally hierarchical nature of the experimental design also allowed for the data to be re-organised by date of collection (a 'simultaneous removal' design). This design enabled studying community assembly in which the seasonal effects of date of collection are controlled in the analysis (Dean and Connell 1987a, Miyake et al. 2003) and in which the role of history in community dynamics can be considered. We also organised the data by community age to test whether there was an approximately consistent endpoint to assembly across deployment/collection dates or whether there were alternative end-states depending on season or recruitment history (Drake 1990).

Univariate and multivariate analyses by date of substratum deployment and collection indicated that season did influence assembly in this type of community. However, if holdfasts were deployed for sufficient time, there was a relatively consistent endpoint to assembly, which varied only gradually (but significantly) with date of collection and, sometimes, with history.

2.3 Methods

2.3.1 Experimental design and field work

Artificial kelp holdfasts (hereafter 'holdfasts') were constructed of bundles of 10, 150-mm lengths of polypropylene rope bound together at one end with a plastic

cable tie. At the other end, the rope strands were separated, splayed and glued to a 100 mm x 100 mm PVC base. The design was similar in size and physical complexity to the holdfasts of *Ecklonia radiata*, the most common species of kelp in southern Australia.

Holdfasts were attached to concrete bricks with cable ties and distributed over sand adjacent to a healthy *E. radiata* dominated reef at ca. 8 m depth in the Derwent River Estuary, Tasmania, Australia (42° 57.7' S, 147° 20.5 E; Figure 1). The study site was 100 m x 4 m, and holdfasts were deployed randomly to 1 m grid co-ordinates. The rocky reef ran the full length (100 m) of the grid and was likely the major source of recruits to the holdfasts. Note that recruits could arise from settling larvae or through migrating adults, although migration of adults was intentionally limited through the isolation of holdfasts on the sand substratum.

Holdfasts were deployed each month for 13 months beginning in December 1997. At each deployment, sufficient holdfasts were established to collect 6 replicate holdfasts each subsequent month until January 1999 (Figure 2). An earlier pilot study indicated that 6 holdfasts was the minimum sampling intensity to adequately estimate natural variability across replicate holdfast communities, standard errors in the abundance of individual taxa did not significantly decrease with a greater number of replicates. Deployment and collection dates were toward the end of the nominated month, weather permitting. Water temperature peaked in January and February at 18°C and reached a minimum of 11°C during June, July and August. A total of 408 holdfasts were deployed to random positions on the grid and later recovered.

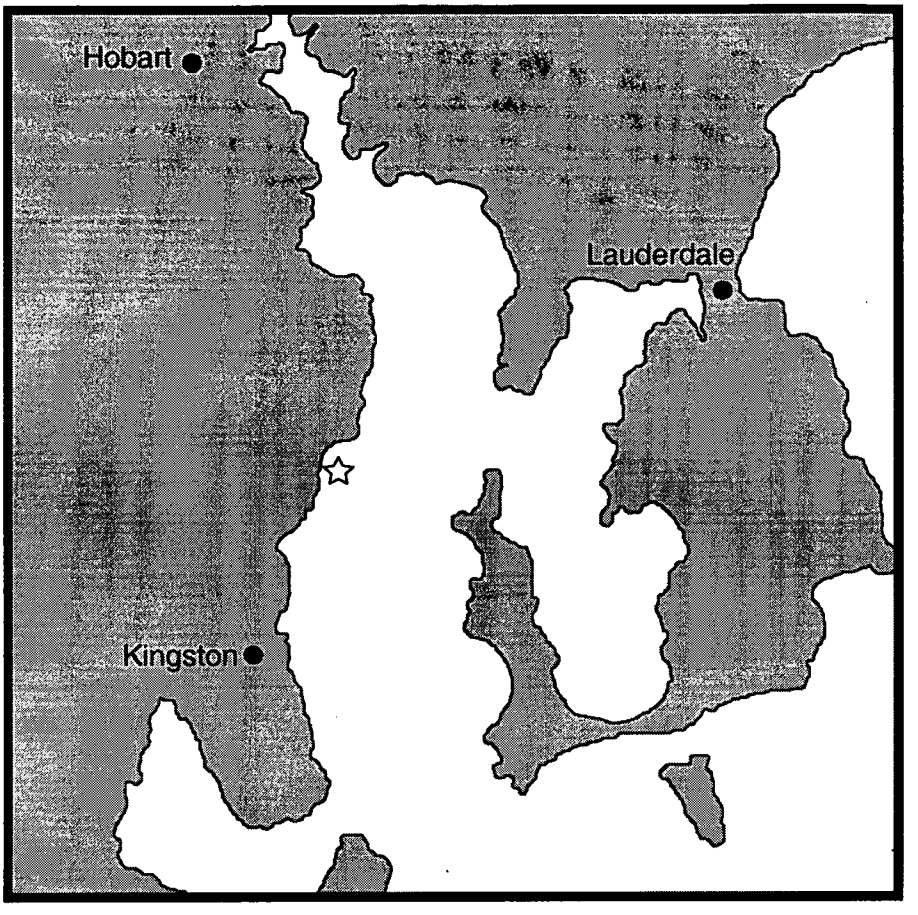

Figure 1 Map illustrating the location of the study site (☆).

Monthly collections involved recovering 6 randomly selected replicate holdfasts from each previous month of deployment. Holdfasts were gently covered with a plastic bag before cutting the cable ties attaching the holdfast to its concrete brick and sealing the bag for transport to the surface. Vacated grid-positions were open to subsequent deployment of another artificial holdfast (if randomly selected). Due to poor weather, holdfasts could not be collected or deployed in September while collections were not possible in June. For treatments deployed in

December 1997, 4 replicates (rather than 6) were collected each subsequent month.

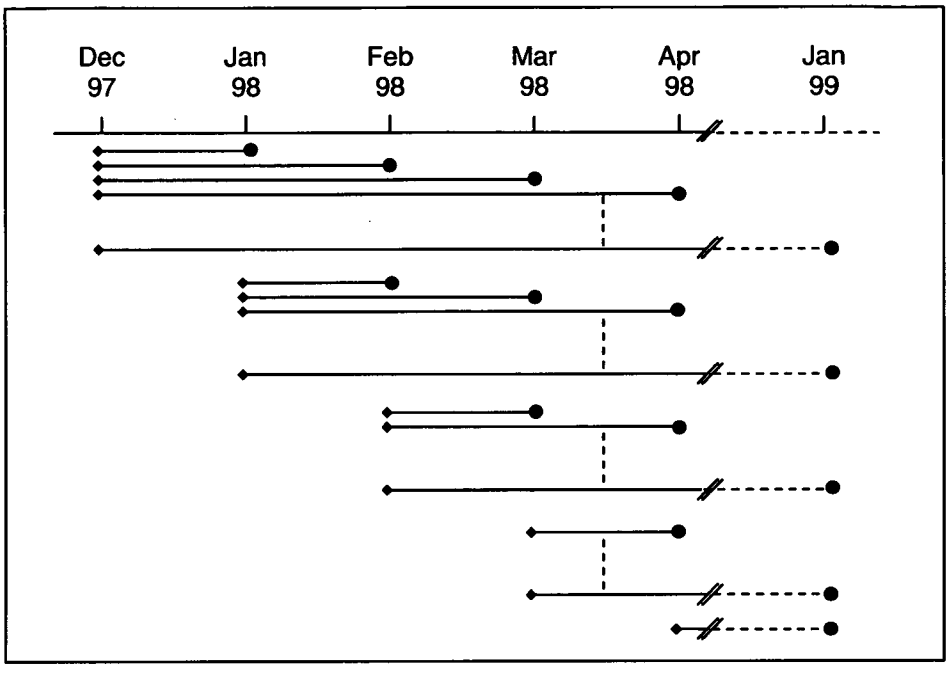

Figure 2 Schematic representation of the sequence of deployment and collection of artificial kelp holdfasts. The entire experiment extended from December 1997 to January 1999. The complete design included 91 different 'treatments', each with unique deployment and collection dates, and there were 6 replicate holdfasts of each 'deployment/collection' combination. Note however, that because of poor weather, We were unable to deploy and retrieve holdfasts exactly to this design (see Methods). Each line represents deployment (⬧) and collection (•) dates of 6 replicate holdfasts. Dotted lines indicate an extended series of deployments not shown in detail.

Holdfasts were preserved in ~5% buffered formalin. For processing, holdfasts were readily broken open (by the cutting of the cable tie) and washed thoroughly over a 1 mm sieve to remove all animals. Solitary animals retained on the sieve were identified where possible to the level of family, the most notable exception being amphipods, which were identified to sub-order. Colonial organisms were not enumerated because they were very rare. We deemed taxonomic resolution to

the level of family as the optimal cost-benefit trade-off given the large abundance of organisms encountered (148,841 individuals), and that family-level patterns typically reflect patterns at the species-level (Williams and Gaston 1994, Faith et al. 1995, James et al. 1995, Somerfield and Clarke 1995, Balmford et al. 1996, Olsgard et al. 1997, Mistri and Rossi 2001, Dahl and Dahl 2002, Olsgard et al. 2003, Anderson et al. 2005a, Anderson et al. 2005b). Note that the level of identification used for the amphipods was sub-optimal since the group would contain a number of functional feeding groups; this unfortunately was unavoidable for the reasons outlined above.

2.3.2 Analysis overview

Community structure and temporal dynamics were analysed using both univariate and multivariate techniques.

2.3.2.1 Univariate indices

Three univariate metrics describing community structure were used: familial richness (total number of families), total abundance of all individuals in a holdfast and Pielou's evenness J' ($J'=H'/log(S)$, Pielou 1969), where $H'=-\Sigma p_i \ ln \ p_i$ (Margalef 1958), S= number of families in the community and p_i=proportion of total sample belonging to the i^{th} family). Indices were calculated for individual holdfasts and then averaged across replicate holdfasts for each deployment/collection date and community age. Where applicable, analysis-of-variance (ANOVA) was used to compare the metrics among different time intervals. Several rank abundance plots were also constructed because the results indicated that communities initiated at different times displayed convergence in their structure as they developed; communities $\geq$ 5 months in age were

consistently located within a defined region of nMDS space. A single community was randomly selected as a reference point to set the order of taxa on the x-axis (the average community deployed in April 1998, community age = 7 months). Rank abundance plots for 3 different subsets of community were then constructed to compare to the reference community; i) the three average communities ≥ 5 months in age that were least similar to the reference community, ii) the three average communities ≥ 5 months in age that were most similar to the reference community and iii) three 'outgroups', three randomly selected average communities < 5 months in age.

Note that we also calculated Shannon-Wiener diversity (*H'*) but since this measure was ineffective in representing temporal variability in community structure results are not presented. *H'* did not vary in response to changes in richness and evenness with time and was poorly correlated (weighted spearman rank correlation coefficient, ρ_w=0.007 ; BIOENV procedure in PRIMER5, Clarke and Ainsworth 1993) with multivariate community structure (while both richness and evenness were relatively well correlated with community structure; ρ_w=0.48). This is because in this community, like many others (Stirling and Wilsey 2001), richness and evenness were negatively correlated ($J' = -0.01S + 0.79$, $R^2 = 0.33$, $P<0.0001$).

2.3.2.2 Multivariate analysis

Bray-Curtis similarity (Bray and Curtis 1957) was used to compare communities of different deployment and collection dates and community age. Replicate holdfasts were first averaged to give an average total abundance for each taxonomic group and then fourth-root transformed to prevent numerically

abundant species from dominating the analysis (Clarke and Green 1988). Average communities were used to reduce the complexity of the resulting nMDS plot. The transformation meant that the multivariate analysis was relatively insensitive to any large influx of naturally abundant taxa. In this circumstance univariate measures were more useful in describing community structure.

Non-metric multi-dimensional scaling (nMDS) plots were used to graphically represent patterns in Bray-Curtis space. PERMANOVA *v1.6* (Anderson 2001, McArdle and Anderson 2001, Anderson 2005) was used to test for effects on mean community structure and/or the spread of communities in Bray-Curtis space. PERMDISP (Anderson 2004) was used to test for effects on the spread of communities in Bray-Curtis space and so was useful in interpreting the significant PERMANOVA test. ANOSIM was used when the design was unbalanced (Clarke and Green 1988). For the PERMANOVA, PERMDISP and ANOSIM analyses, data were from individual holdfasts so that variability among replicate holdfasts could be estimated.

2.3.3 Community assembly by date of deployment and date of collection

Community assembly trajectories were constructed for each deployment date, on the basis of richness, total abundance, evenness, and community structure in Bray-Curtis space. Due to the hierarchical nature of the design and missing data, the interaction between date of deployment and community age could only be tested using PERMANOVA and PERMDISP for the first three dates of deployment (December 1997 – February 1998) and for communities up to 3

months in age. Community assembly trajectories were similarly constructed for each collection date.

2.3.4 Community assembly: comparison of endpoints

Results of analyses conducted by date of deployment and by date of collection indicated that community structure converged as communities developed. By 5 months of development, community structures were broadly consistent across treatments regardless of the date of deployment or collection. Communities of the same age were compared statistically to determine whether this 'endpoint' in assembly was the same irrespective of the dates of deployment and collection. Only communities ≥ 5 months of age were included in this analysis to remove the effect of community development. ANOVA (for univariate measures of community structure) and ANOSIM (for multivariate measures of community structure) were used to determine the statistical significance of differences among deployment and collection dates. When necessary data were log transformed prior to ANOVA to stabilise variances. Significant overall ANOVAs were followed by Ryan-Einot-Gabriel-Welsch *post-hoc* tests (REGWQ; in SAS *v 6.12*) to identify the nature of significant differences.

2.4 Results

2.4.1 Community assembly by date of deployment

Community trajectories varied significantly across the different deployment dates for both univariate and multivariate measures of community structure (Figures 3-6). The accumulation of families (richness; Figure 3) and individuals (total abundance, Figure 4) occurred more quickly in seasons with warmer water

temperature compared to those characterised by cooler water and so young communities developed during warm months were more likely to resemble older communities than communities of similar age that developed during winter.

Across all communities, total abundance (*ta*) correlated closely with familial richness (S=3.25.$ta^{0.33}$, R^2=0.85). Average richness peaked between 25-30 families per holdfast (Figure 3), while average total abundance usually peaked between 500-750 individuals per holdfast (Figure 4). While communities that established in warmer months attained maximum (or close to) abundances and richness within 1 to 3 months, communities initiated in cooler months took as long as 5 months to reach the same stage (Figures 3 and 4).

As communities aged, the relative abundances of the different families also varied and this was reflected in patterns in evenness. Evenness remained relatively unchanged through time for communities established in warmer months (Figure 5). However, communities established in cooler months initially showed higher values of evenness, which decreased with community age to values similar to those reported in summer (~0.5-0.6; Figure 5).

Community structures converged to a broad region in nMDS space regardless of the date of deployment (Figure 6). Communities within this 'domain of attraction' were characterised by high familial richness and total abundance, but slightly lower evenness, than communities located outside of this space (Figures 3-5). Rank abundance plots indicated that the there were some similarities in familial abundances among these communities (Figure 7). Communities within this region of nMDS space showed similar patterns of rank abundance to each

other, but not to communities located outside of this region of nMDS space (Figure 7). For brevity, this region of nMDS space is termed an 'endpoint' to assembly. However, the region is broad relative to the total nMDS space and likely to incorporate a spectrum of community types.

While the endpoint to assembly for the multivariate community analysis was similar regardless of time of deployment, the trajectory to this region of nMDS space was distinctively different depending on deployment date (Figure 6a-f). Initial communities establishing during cool months were most dissimilar to those characterising the assembly endpoint, however, they had developed to this 'mature' community configuration by 5 months of age (Figure 6d-e).

Communities initiated in warmer months reached the configuration of a mature community in less time (Figure 6b-c). This dynamic yielded a significant interaction between the date of deployment and community age in influencing multivariate community structure ($F_{4,27}$=2.15, P=0.0004; PERMANOVA on communities established between December and February and up to 3 months of age). This was at least partly due to significant differences in the variability of community structure among treatments ($F_{4,27}$= 4.33, P=0.002; PERMDIST).

An interesting result was obtained for holdfasts deployed in June and July 1998 and collected in January 1999 (community age = 7 and 6 months, respectively). On average, more individuals established on these holdfasts than on most others, including on those that were established in summer months and those that were deployed for shorter and longer time intervals (Figure 4). This increase in total

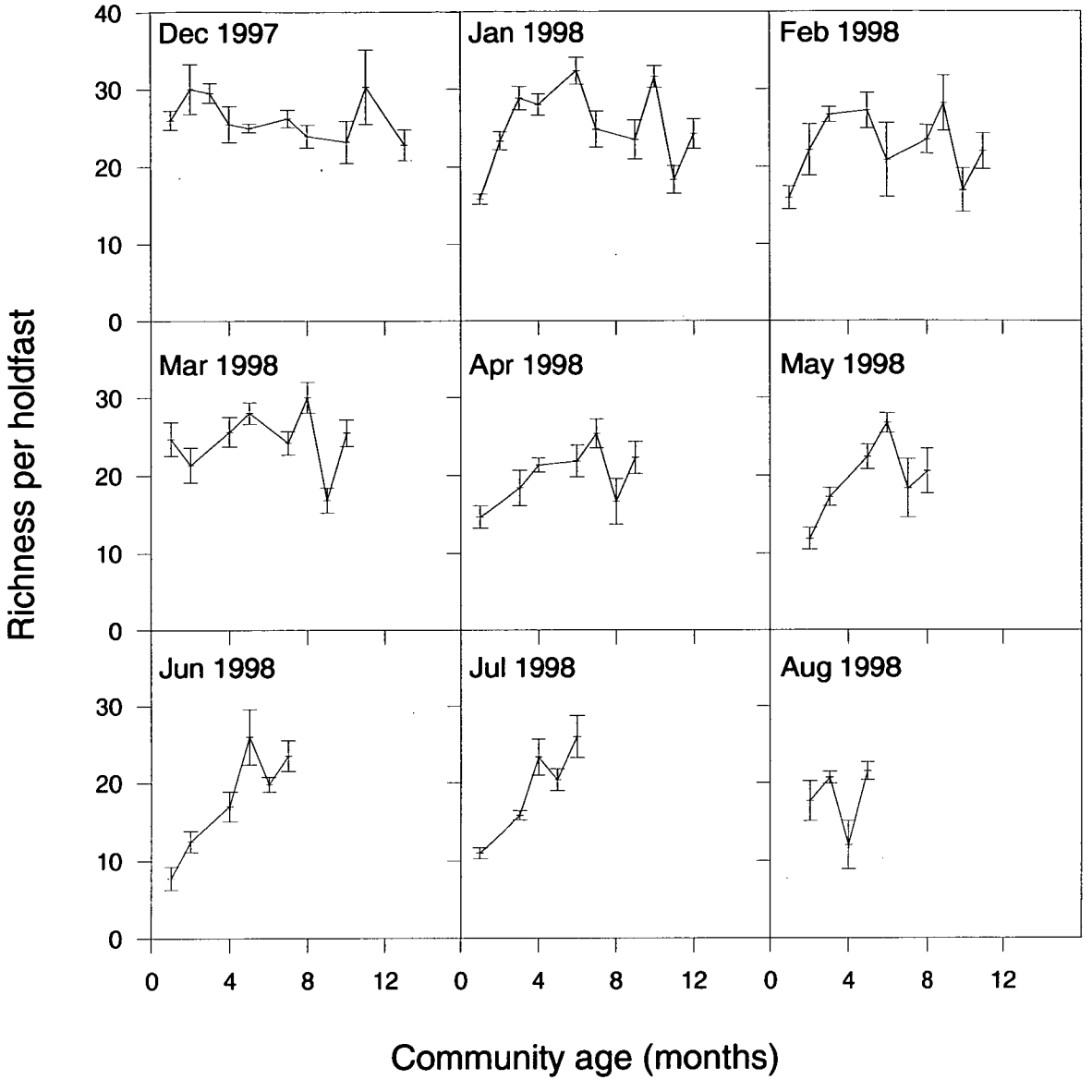

Figure 3 Average familial richness (± standard error) of different aged communities for successive monthly holdfast deployment dates from December 1997 through to August 1998. Note that because the experiment concluded in January 1999, there were too few data points to obtain a meaningful description of community assembly for deployment dates between October 1998 and December 1998. Note also that the number of replicates for communities deployed in December 1997 was 4 rather than 6.

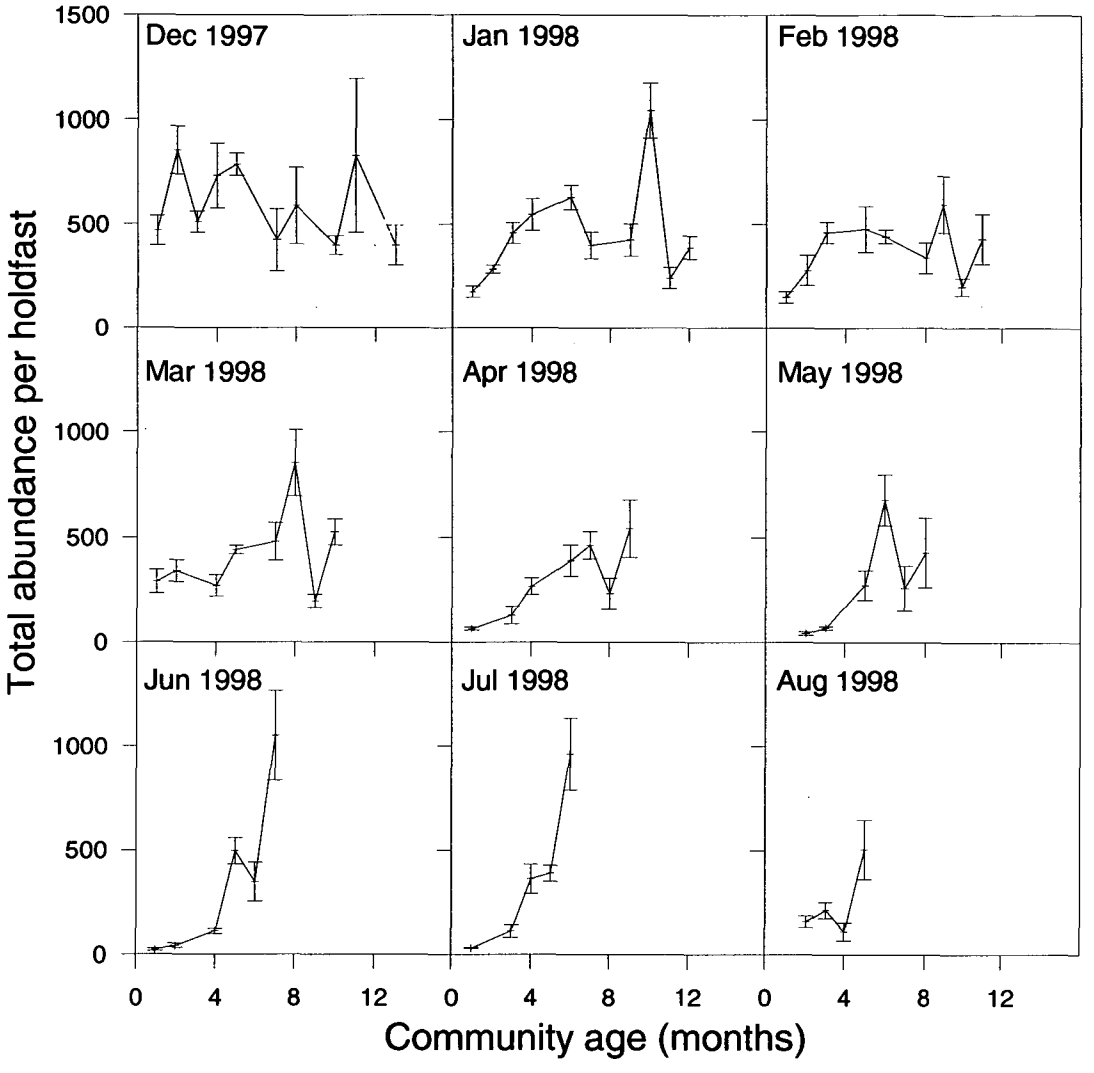

Figure 4 Average total abundance (± standard error) of different aged communities for successive monthly holdfast deployment dates from December 1997 through to August 1998. Note that because the experiment concluded in January 1999, there were too few data points to obtain a meaningful description of community assembly for deployment dates between October 1998 and December 1998.

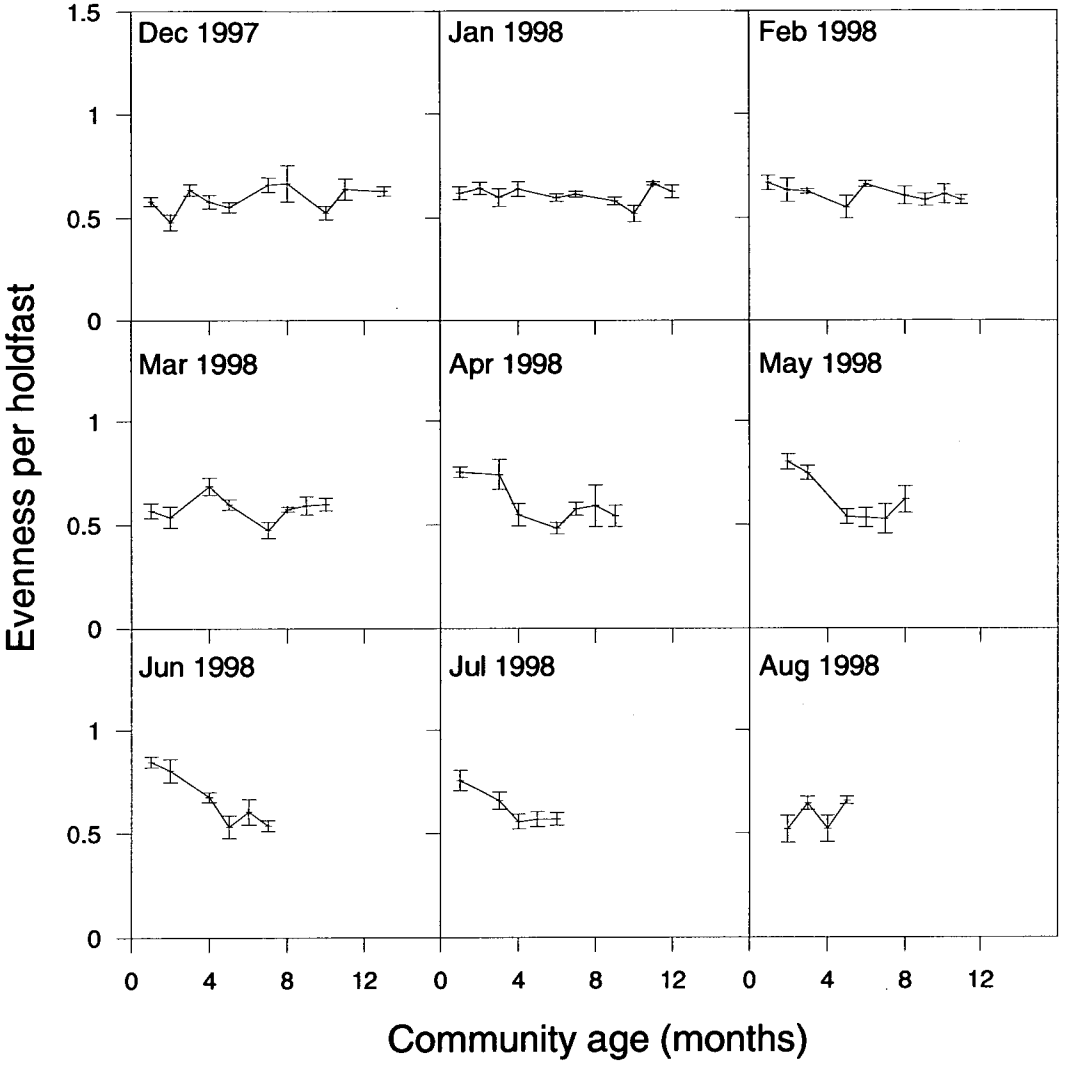

Figure 5 Average evenness (± standard error) of different aged communities for successive monthly holdfast deployment dates from December 1997 through to August 1998. Note that because the experiment concluded in January 1999, there were too few data points to obtain a meaningful description of community assembly for deployment dates between October 1998 and December 1998.

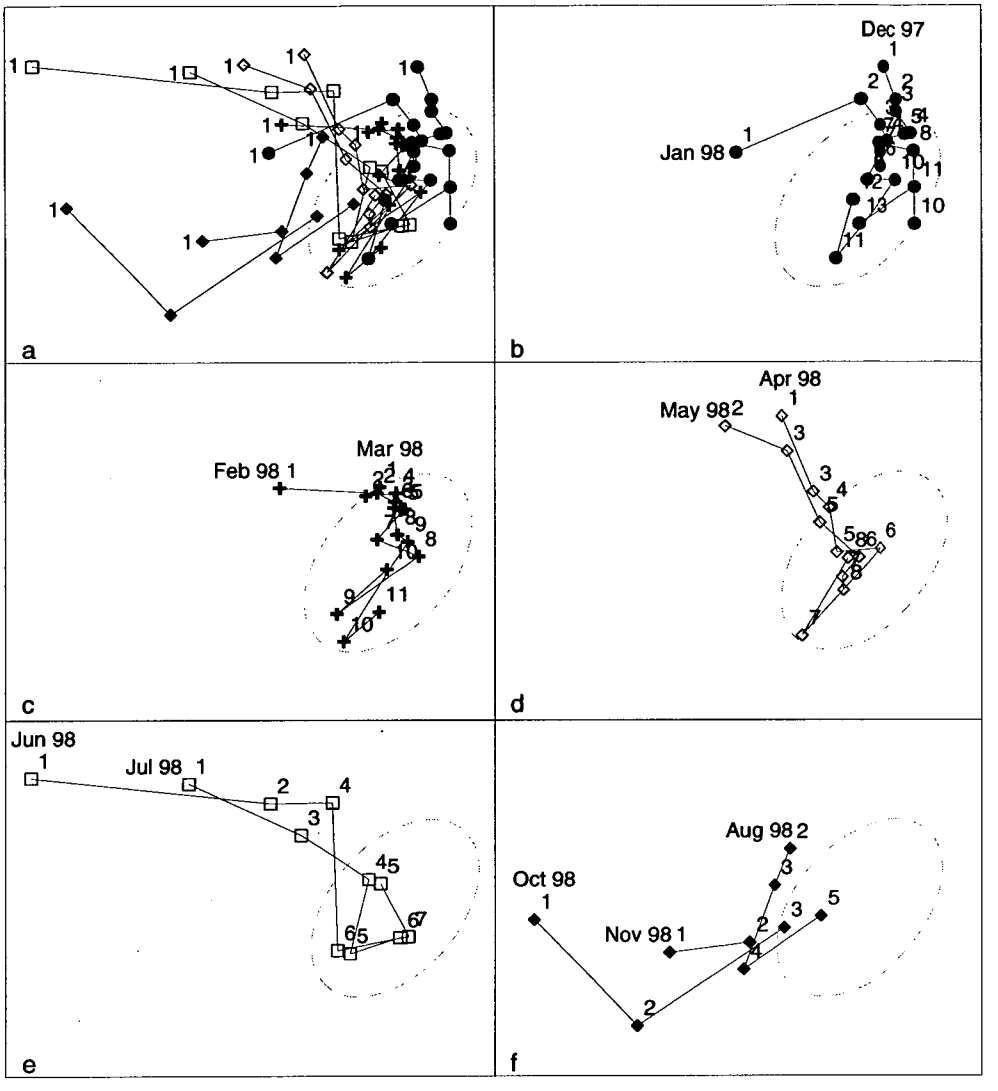

Figure 6 NMDS plot representing patterns in Bray-Curtis similarity (based on fourth-root transformed data) for average communities of different deployment dates and of different community age (Stress =0.17). Trajectories are labeled to illustrate the pathway of a community through time for each deployment date. Numbers represent the age of a community, and trajectories begin with 1-month-old communities. (a) all deployment dates; deployment dates of (b) December 1997 and January 1998 (solid circles); (c) February and March 1998 (crosses); (d) April and May 1998 (open diamonds); (e) June and July 1998 (open squares); and (f) August, October and November 1998 (solid diamonds). The deployment date of December 1998 is not presented because the experiment concluded in January 1999. Ellipses within each plot were created to illustrate the region of the nMDS plot that bounded all communities ≥5 months in age.

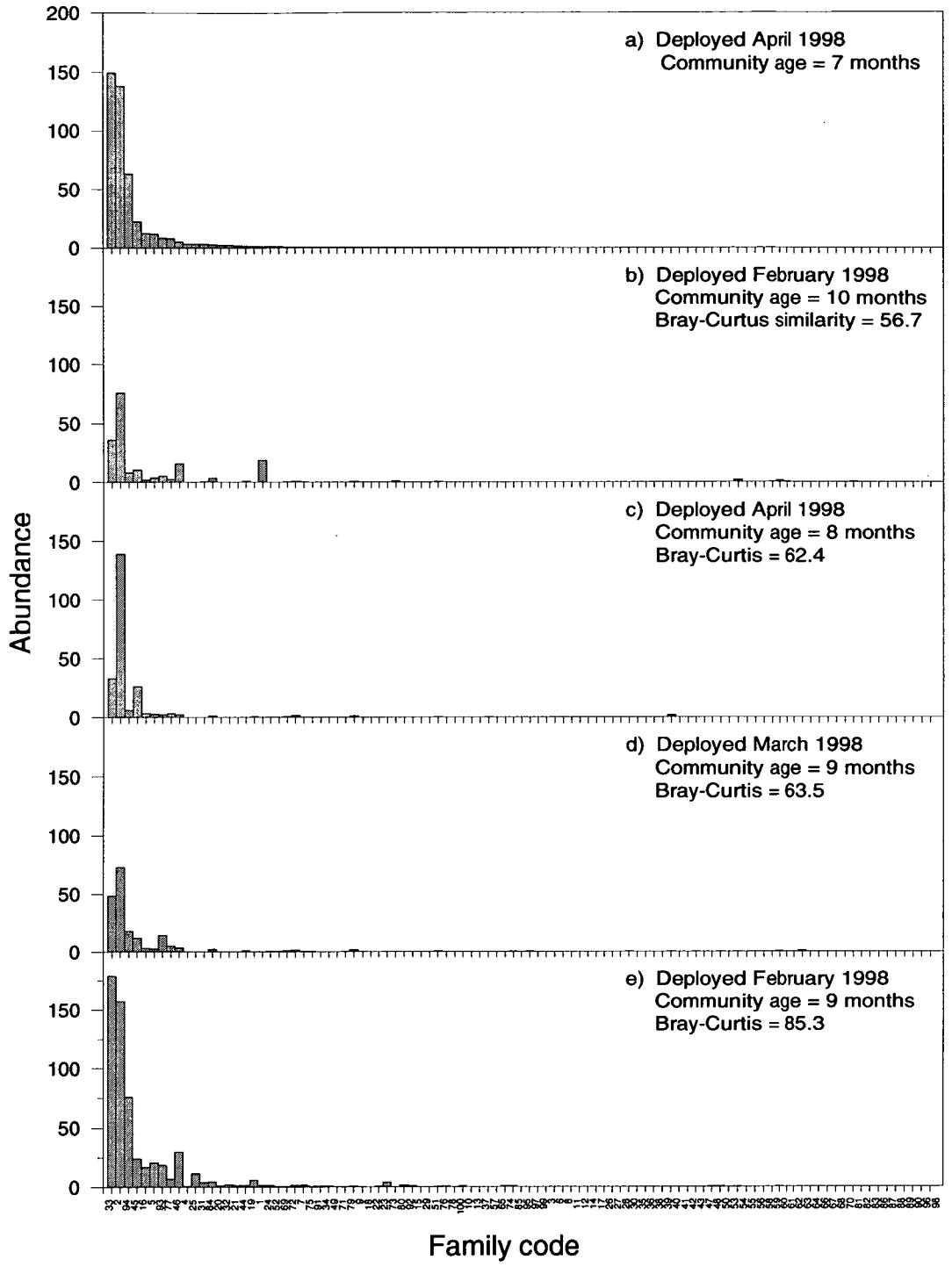

Figure 7 Rank abundance plots for a selection of average communities. (a) a randomly selected reference community deployed in April 1998, community age = 7 months; this plot was used to determine the order of families on the x-axis; (b)-(d) the 3 average communities of an age ≥5 months, that were least similar to the reference community; (e)-(f) the 3 average communities of an age ≥5 months, that were most similar to the reference community; (g)-(i) 3 randomly selected communities of an age <5 months. Bray-Curtis similarities are calculated on the fourth-root transformed data and represent the percent similarity between the reference community and all other communities. Family codes are translated in Appendix 1.

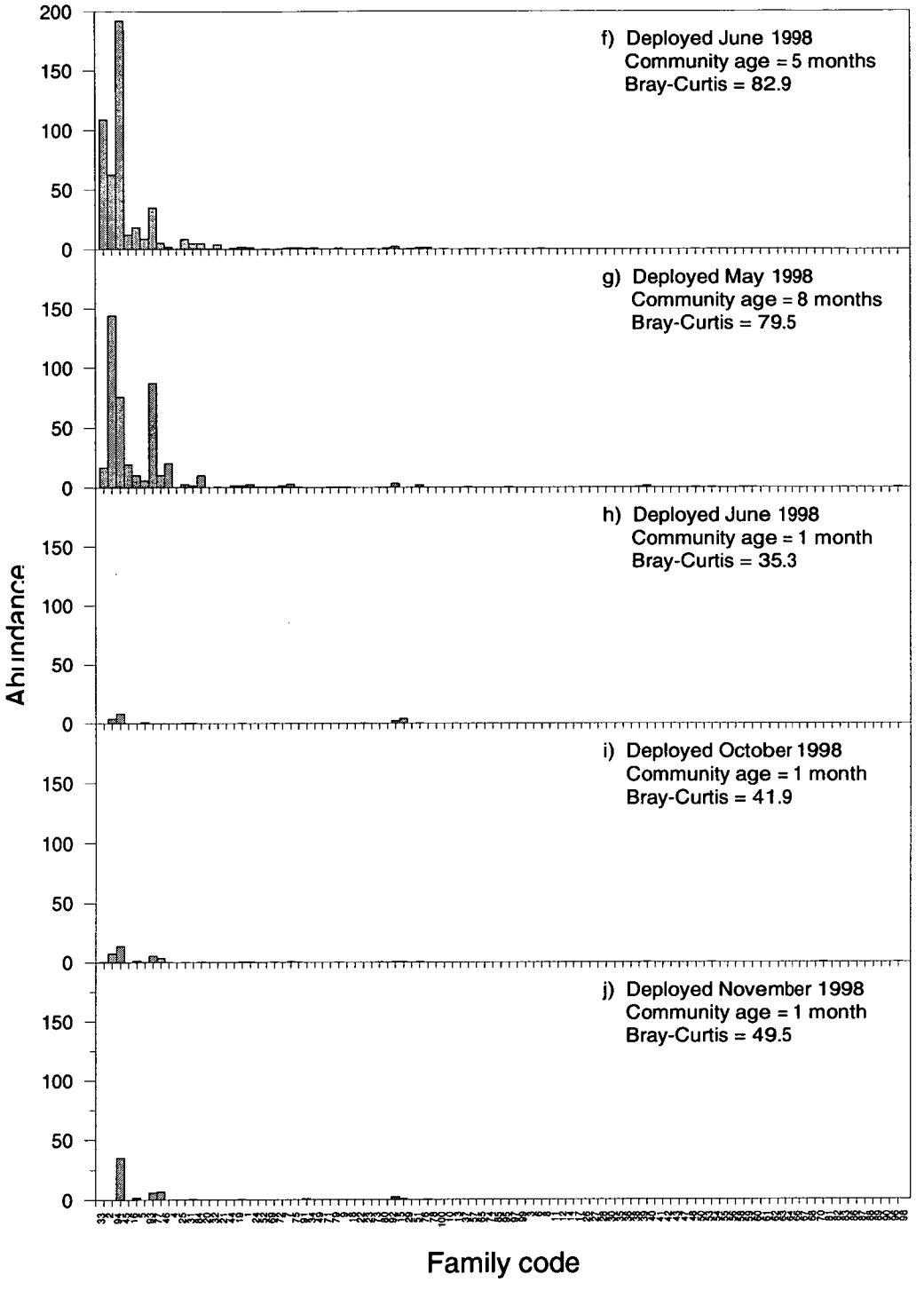

Figure 7 continued.

abundance was not accompanied by any increase in familial richness (Figure 3), but there was evidence of a slight decrease in evenness (Figure 5), indicating that individuals of a small number of taxonomic groups dominated these communities. The highly abundant taxa in these holdfasts were gammarid and caprellid amphipods and, to a lesser extent, isopods of the family Arcturidae.

2.4.2 Community assembly by date of collection

Results for the analysis by date of collection were similar to those obtained for the analysis of community assembly by date of deployment. For example, communities developed towards an assembly endpoint, community trajectories varied significantly across the different collection dates (warmer months accumulated families and individuals more quickly than cooler months), and the endpoint in assembly was similar, for both univariate and multivariate measures of community structure (Figures 8-11). However, analysis by date of collection also provided additional insight about community assembly and variation.

For the collection date of January 1999, average total abundance in holdfasts was less than 500 individuals for all deployment periods (1 month - 13 months), except for the 6 and 7 month old communities (Figure 9). The 6 and 7 month-old holdfasts were numerically dominated by relatively few taxonomic groups (as identified in the analysis by date of deployment). Holdfasts deployed at the same time as the 6 and 7 month-old communities, but collected one time step earlier (5 and 6 month-old holdfasts collected in December 1998), showed a slightly elevated total abundance compared to other holdfast communities collected at the same time. However, they were not dominated by a small number of taxa (unlike the 6 and 7 month-old communities richness increased with the increase in

abundance; Figure 8). It follows that most individuals of these crustaceans that came to dominate these communities arrived in January 1999. Note that other holdfasts collected at the same time in January 1999 were presumably also exposed to these same recruits (whether juveniles or migrating adults), yet only those holdfasts deployed in June and July allowed them to establish *en masse*. These communities are not distinct in nMDS space from others of the same age (Figures 6 and 11) probably because data were fourth-root transformed prior to the nMDS which reduced the influence of the numerically abundant taxa.

The region containing the assembly endpoint for each of the deployment dates was large relative to the total nMDS space describing all holdfast communities (Figures 6 and 11). However, a component of this variability could be explained by the date of collection of holdfasts since there was a directional shift in the assembly endpoint across nMDS space when holdfasts were labelled by date of collection rather than date of deployment (Figure 11).

2.4.3 Comparison of community assembly endpoints

Communities ≥5 months in age deployed for the same time interval but at different dates showed clear differences in richness, total abundance, evenness, and Bray-Curtis similarity (Table 1). While some of these differences were significant, there were no consistent trends in univariate measures of community structure, suggesting that these differences were not entirely due to date of deployment or collection (Figures 12-14). In contrast, analysis of Bray-Curtis similarity indicated consistent significant differences between holdfasts deployed for the same time interval but at different dates. This was probably due in part to the directional variation seen in the endpoint to assembly with date of collection

(observed in Figure 11), although significant ANOSIM results may also indicate a significant difference in the degree of spread of communities in Bray-Curtis space among treatments.

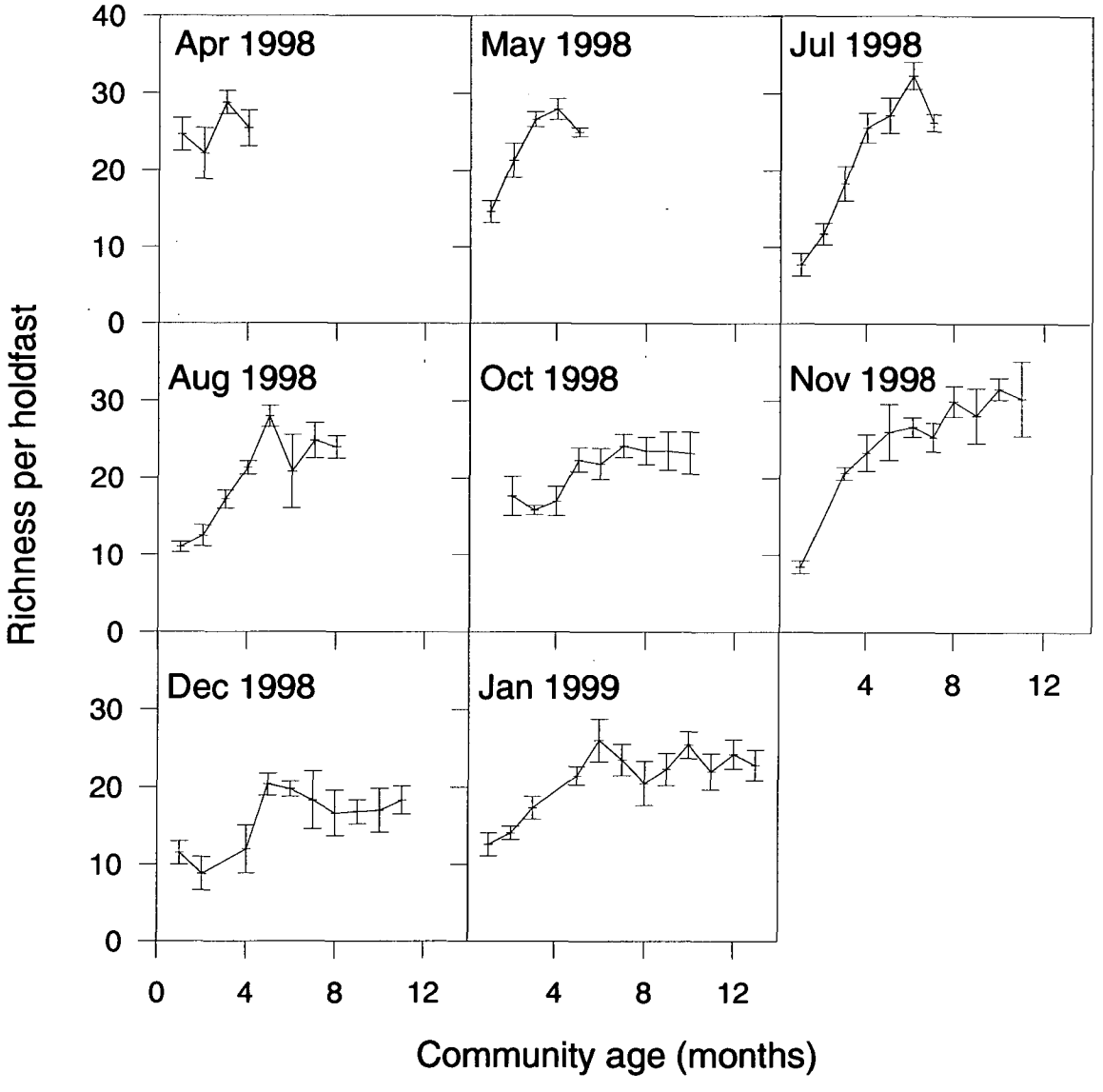

Figure 8 Average richness (± standard error) of different aged communities for successive monthly holdfast collection dates from April 1998 through to January 1999. Note that because the experiment began in December 1997, there were too few data points to obtain a meaningful description of community assembly for collection dates between January and March 1998.

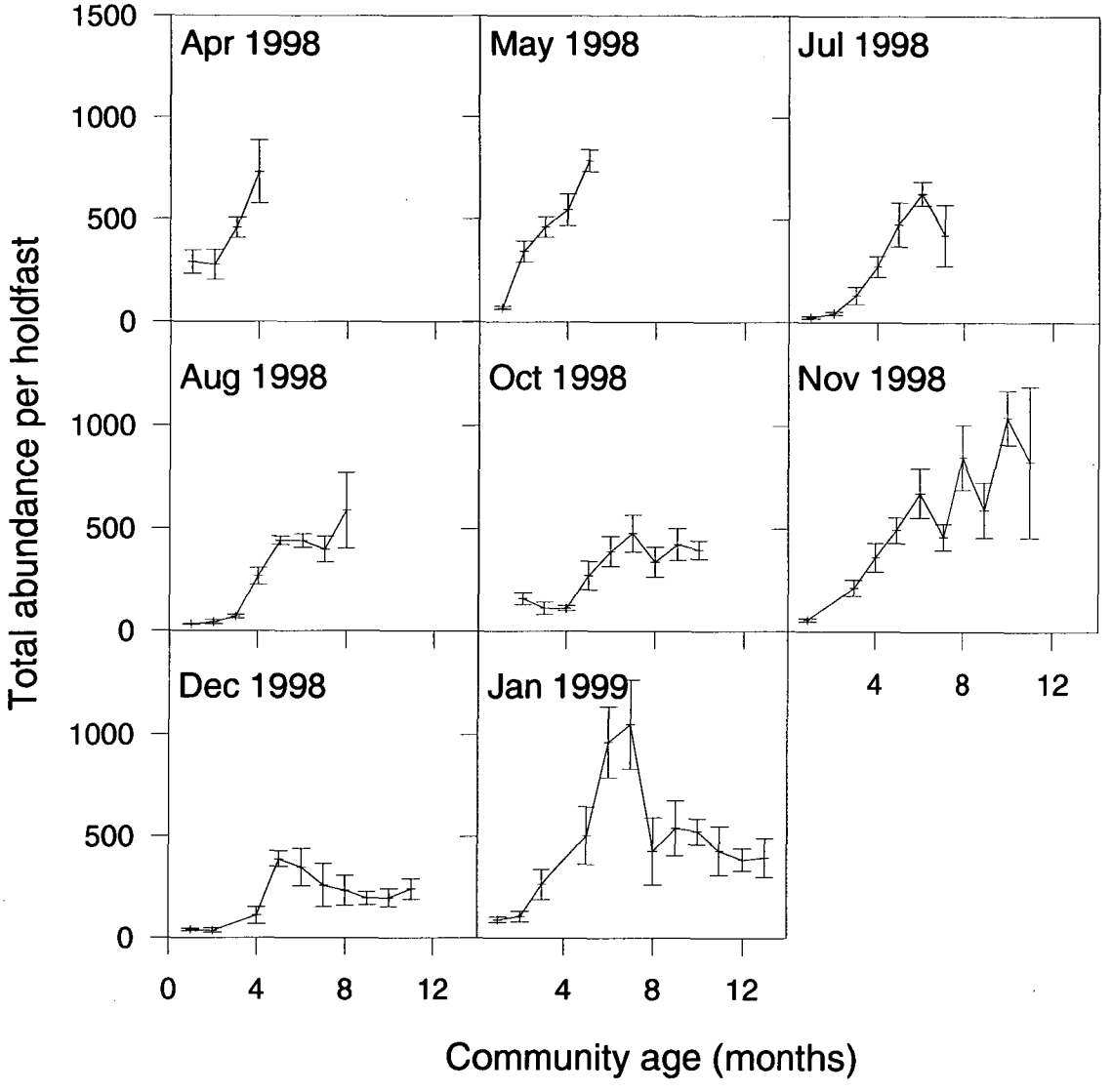

Figure 9 Average total abundance (± standard error) of different aged communities for successive monthly holdfast collection dates from April 1998 through to January 1999. Note that because the experiment began in December 1997, there were too few data points to obtain a meaningful description of community assembly for collection dates between January and March 1998.

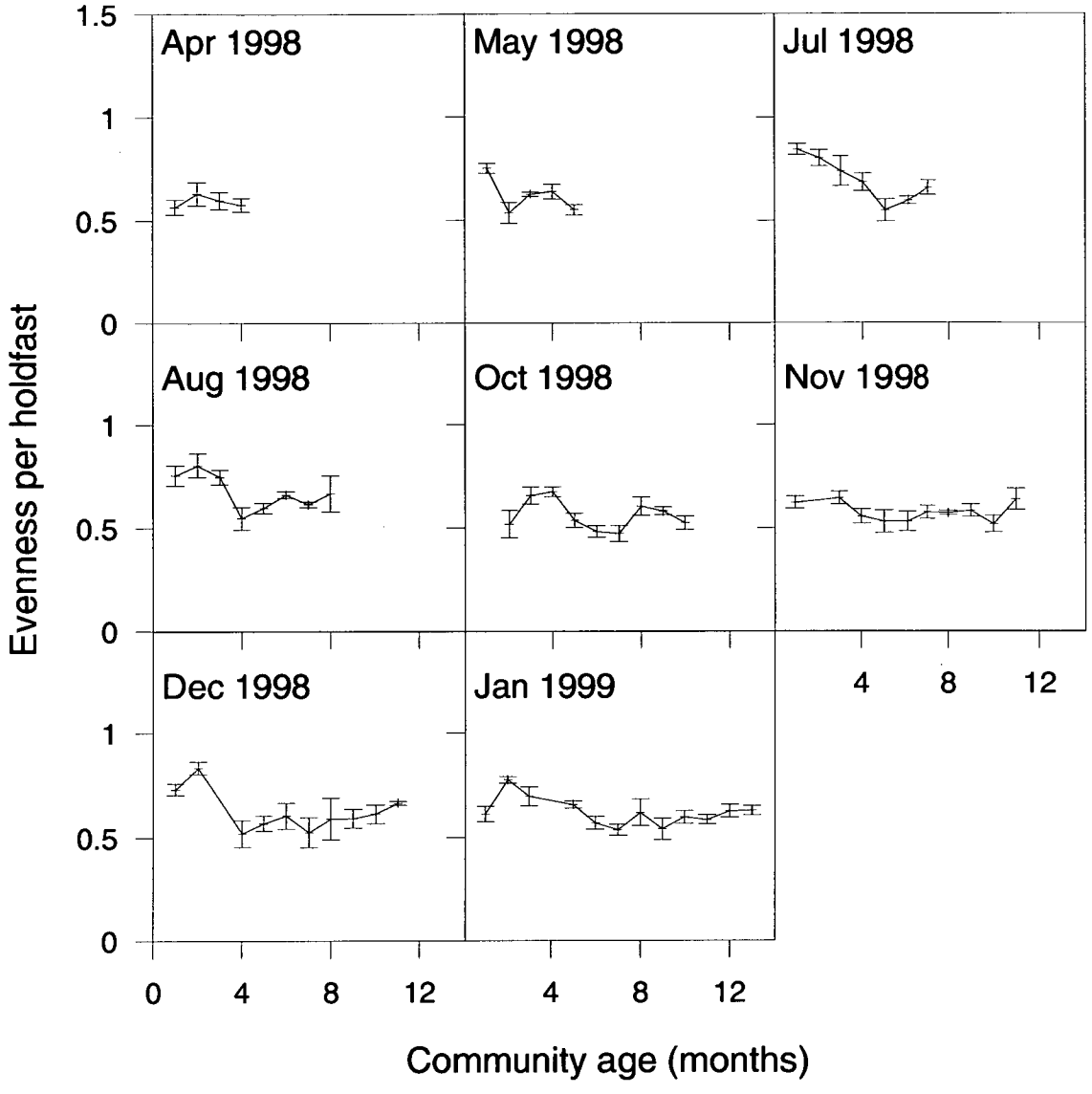

Figure 10 Average evenness (± standard error) for different aged communities for successive monthly holdfast collection dates from April 1998 through to January 1999. Note that because the experiment began in December 1997, there were too few data points to obtain a meaningful description of community assembly for collection dates between January and March 1998.

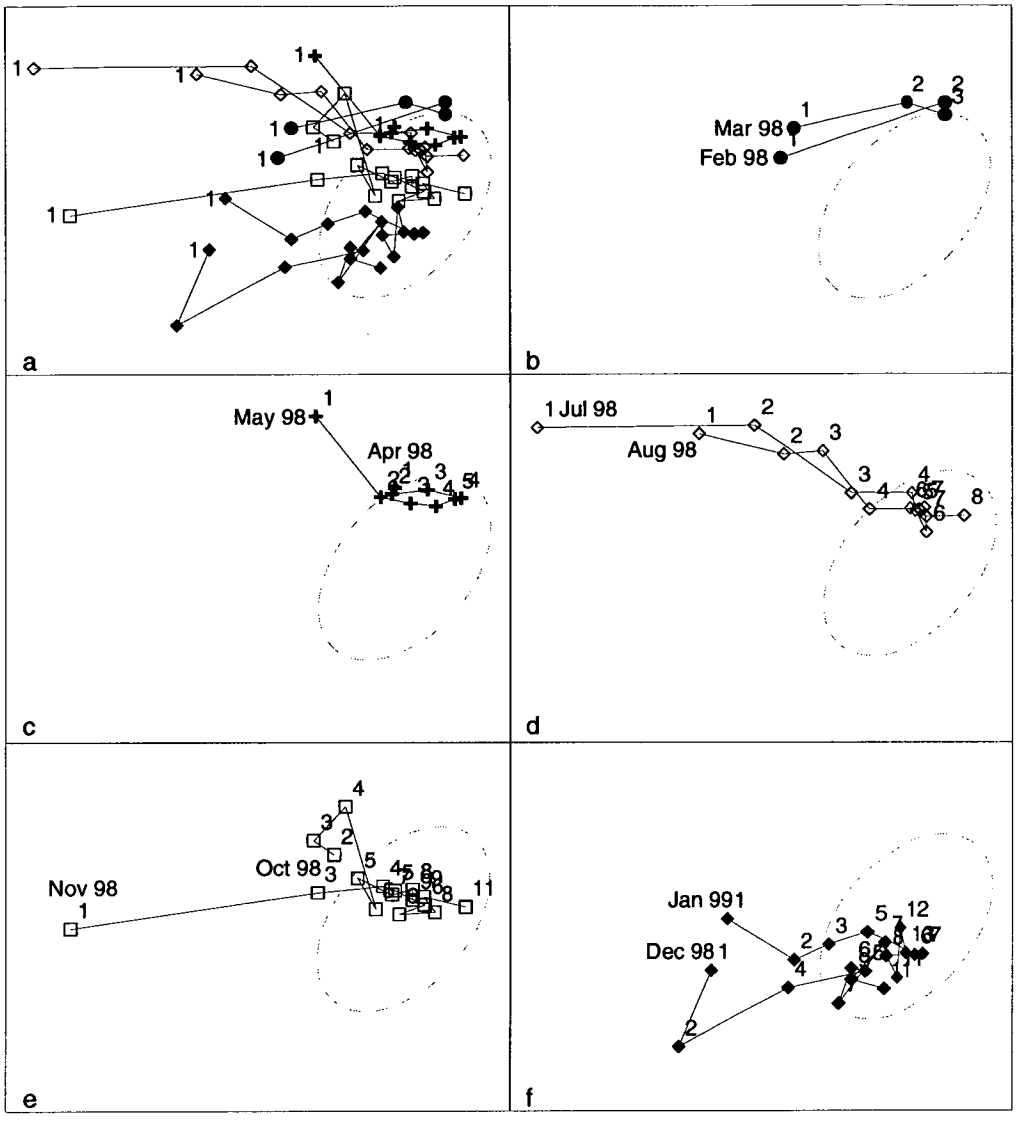

Figure 11 NMDS plot representing patterns in Bray-Curtis similarity (based on fourth-root transformed data) for average communities of different collection dates and of different community age (Stress =0.17). Trajectories are labeled to illustrate the pathway of a community through time for each collection date. Numbers represent the age of a community in months, and trajectories begin with 1-month-old communities. (a) all collection dates; and collection dates of (b) February and March 1998 (closed circles); (c) April and May 1998 (crosses); (d) July and August 1998 (open diamonds); (e) October and November 1998 (open squares); and (f) December 1998 and January 1999 (closed diamonds). The collection date of January 1998 is not presented because the experiment began in December 1997. Ellipses within each plot were created to illustrate the region of the nMDS plot that bounded all communities ≥5 months in age.

Table 1 Analyses contrasting richness, total abundance (T.Abund) and evenness (using ANOVA), and Bray-Curtis similarity (using ANOSIM) among groups of holdfasts deployed for the same length of time but with different dates of deployment and collection dates. Analyses were conducted for immersion times of 5-10 months. Significant probabilities ($P<0.05$) are indicated in bold.

	Age of community (months)					
	5	6	7	8	9	10
ANOVA						
d.f.	6,30	5,29	5,28	4,21	3,20	3,16
Richness						
F	2.54	2.92	1.42	4.95	3.18	6.41
P	**0.041**	**0.030**	0.247	0.057	**0.046***	**0.005**
T.Abund.						
F	1.81	2.75	4.42	2.08	3.19	16.15
P	0.130	**0.038***	**0.004***	0.120*	**0.046***	**0.0001**
Evenness						
F	1.47	3.04	2.37	0.25	0.2	1.23
P	0.223	**0.025**	0.065	0.908	0.892	0.332
ANOSIM						
Global R	0.529	0.601	0.386	0.397	0.335	0.591
P	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**

* Data required log transformation prior to analysis

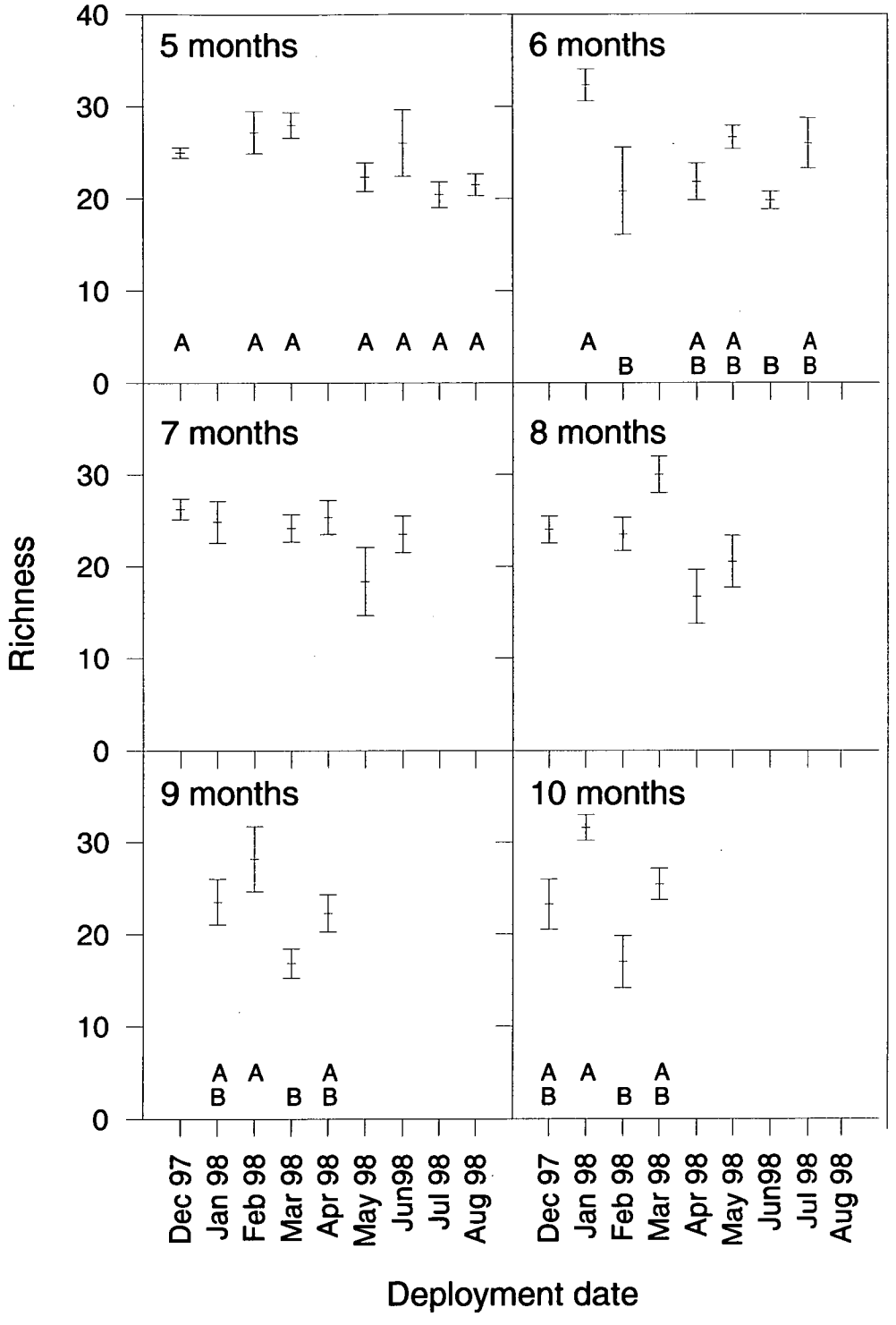

Figure 12 Average richness (± standard error) of communities deployed on different dates for deployment periods of 5-10 months. Letters represent *post-hoc* groupings using REGWQ for comparisons where ANOVA indicated a significant overall effect of 'deployment date' (Table 1). Communities of an age less than 5 months are not presented because these communities were shown to differ with date of deployment because of seasonal effects on the assembly process. Communities of an age greater than 10 months are not presented because there were too few data points for comparison. Note that the number of replicates for communities deployed in December 1997 was 4 rather than 6.

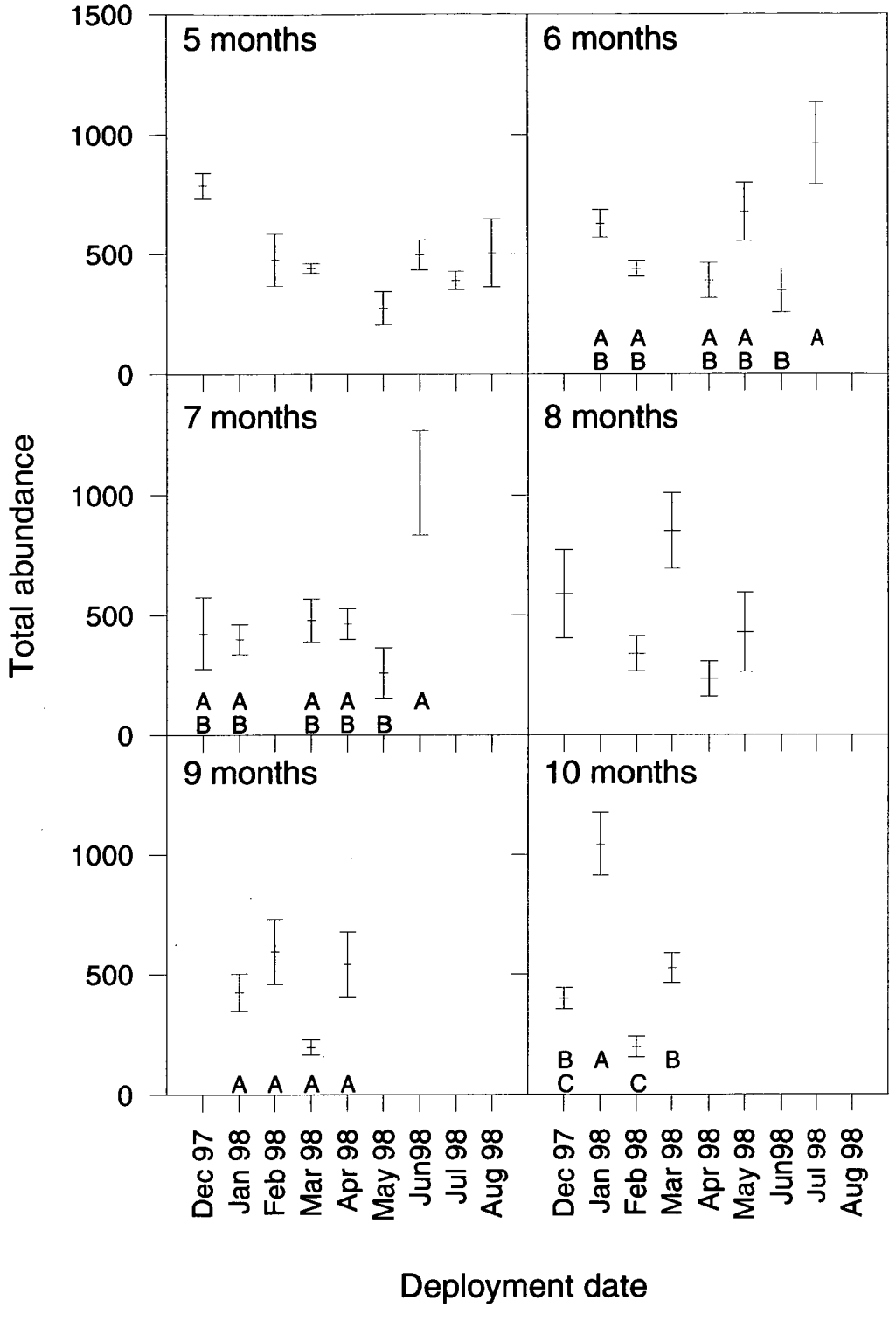

Figure 13 Average total abundance (± standard error) of communities deployed on different dates for deployment periods of 5-10 months. Letters represent *post-hoc* groupings using REGWQ for comparisons where ANOVA indicated a significant overall effect of 'deployment date' (Table 1). Communities of an age less than 5 months are not presented because these communities were shown to differ with date of deployment because of seasonal effects on the assembly process. Communities of an age greater than 10 months are not presented because there were too few data points for comparison.

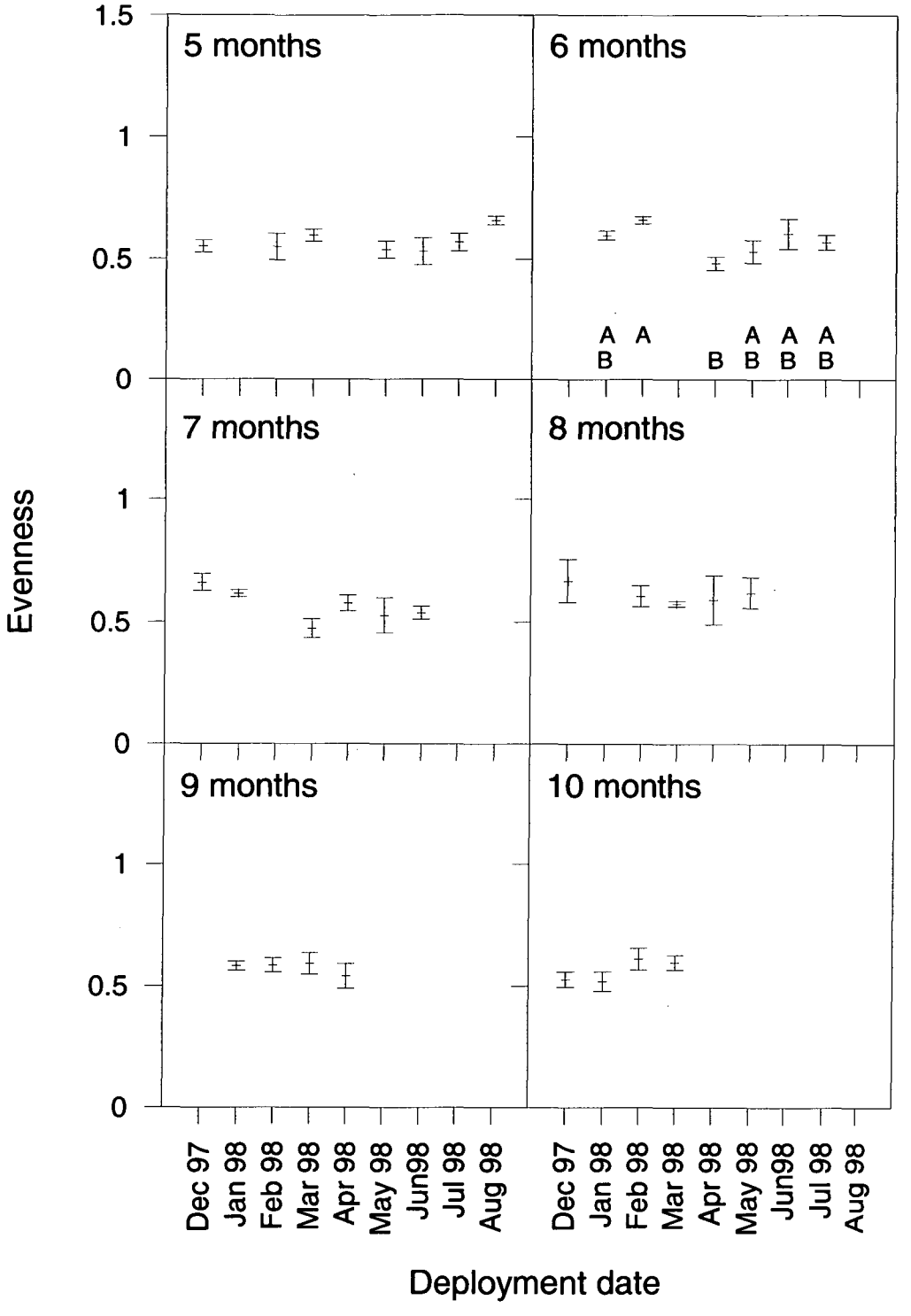

Figure 14 Average evenness (± standard error) of communities deployed on different dates for deployment periods of 5-10 months. Letters represent *post-hoc* groupings using REGWQ for comparisons where ANOVA indicated a significant overall effect of 'deployment date' (Table 1). Communities of an age less than 5 months are not presented because these communities were shown to differ with date of deployment because of seasonal effects on the assembly process. Communities of an age greater than 10 months are not presented because there were too few data points for comparison.

2.5 Discussion

We monitored the effects of season and assembly history on the assembly of artificial kelp holdfast macrofauna communities at monthly intervals over a period of 13 months using a temporally hierarchical sampling design and both univariate and multivariate analyses. Overall findings on assembly were similar regardless of the approach to the analysis, although some univariate measures were more highly correlated with multivariate patterns than others. The experimental design enabled comparison of community trajectories for substrata deployed on different dates, and thus subject to different recruitment regimes. The hierarchical nature of the design also allowed the data to be re-organised for analysis by date-of-collection and by community age. Analysis by date-of-collection provided two further insights to community assembly that could not be obtained from analysis by date of deployment. Firstly, analysis by date of collection indicated that variability in the endpoint to assembly for different start dates was due in part to variation in the date of collection, and secondly indicated that historical factors were important for holdfasts collected in January 1999.

2.5.1 The importance of season

Predictably (based on for example, Dayton et al. 1984, Chapman and Johnson 1990, Underwood and Anderson 1994, Nandakumar 1996), season (i.e. deployment date) was an important determinant of community structure and dynamics in young communities (≤5 months old). However, despite large differences in the abundance and composition of recruits between months, the assembly process realised a community trajectory to a broadly similar domain of

attraction within ~5 months regardless of deployment or collection date. Communities established in warmer months accumulated richness and total abundance more quickly than communities established in cooler months and thus reached the domain of attraction in assembly, or assembly endpoint in less time (1-3 months). This is consistent with the results of several other studies utilizing artificial habitats to sample macrofauna communities (Costello and Myers 1996, Gee and Warwick 1996, Underwood and Chapman 2006). This 'endpoint' to assembly was broadly similar across different deployment and collection dates and community ages (for ages ≥5 months) indicating that community structure is not determined solely by recruitment dynamics. Where the endpoint to assembly was variable (within the domain of attraction), this variability was never correlated with the season of deployment but did appear sensitive to the date of collection.

2.5.2 The importance of history

History was important and manifested as variability in the endpoint to assembly that could not be explained by season of deployment. Its importance was particularly demonstrated in the results for the collection date of January 1999, which varied markedly according to date of deployment. This result indicates that holdfasts deployed 6-7 months prior to this collection date (during June and July 1998) were either influenced by founder effects that were only discernible in January 1999 (*e.g.* seasonal founder effects linked with the date of deployment and collection), or were more receptive to recruitment of particular taxa during January 1999 than holdfasts deployed in the months before or after these deployment dates. Founder effects have been reported in peracarid crustaceans in natural holdfasts of other kelp species (Thiel and Vásquez 2000), because

peracarid crustaceans develop directly and because individuals found in kelp holdfasts may not be as mobile as those found in more dynamic habitats (Thiel and Vásquez 2000). However, the mechanism seems more complex since communities deployed either earlier or later than June and July and collected in January 1999, did not display similar peaks in abundances of gammarid and caprellid amphipods and other Crustacea during January 1999. If the second mechanism is correct, then recruits arriving in January 1999 were either strongly attracted to communities of this age (6-7 months) or inhibited by either competition/predation or a lack of settlement cues in communities of all other ages. The families present in such large numbers on these holdfasts were likely to contain a high proportion of grazing species, and so the mechanism for dominance may also relate to the enhancement or inhibition of the recruitment of a food source such as red algae. Others have noted that macrofauna community structure varies with the successional development of algal communities (Dean and Connell 1987a, b, c).

The mechanism for the dominance of these few taxa may also relate to the use of artificial habitats in this study. The advantages of using artificial substrata to monitor macrofauna communities and environmental impact are well described. Communities that establish on artificial substrata are less variable than communities on natural equivalents (Edgar 1991b), are easier to collect, and can be controlled for the effects of community age, times of deployment and collection, disturbance history and the many other factors known to contribute to variability in macrofauna communities. The communities that establish in kelp holdfasts are a well documented example of high variability arising in communities developed on natural substrata (Smith et al. 1996, Goodsell et al.

2004, Anderson et al. 2005a, Anderson et al. 2005b). Despite these advantages, the use of artificial substrata as monitoring devices also has limitations. Communities established on artificial substrata often lack the characteristics of their natural counterparts, for example they are frequently numerically dominated by a few strong competitors and lack diversity (*e.g.* Edgar 1991a, Underwood and Anderson 1994, Wahl 2001, Kelaher 2002, Smith and Rule 2002). Smith and Rule (2002) suggested that opportunistic taxa may be able to recruit and persist on artificial substrata because there are too few predators and/or competitors at the time of their recruitment. Further study of the importance of history is necessary for these types of communities if artificial habitats are to be used as surrogates for natural kelp holdfast communities, since grazing invertebrates are capable of having large impacts on marine benthic community structure (Duffy and Hay 2000).

It should be noted that while in our case (and in several other studies *e.g.* Kelaher 2002, Edgar and Klumpp 2003), it was invariably crustaceans that dominated communities in circumstances where abundances were most strongly skewed, others working on similar macrofauna communities using artificial substrata found dominance by other taxonomic groups (*e.g.* sedentary polychaetes, Smith and Rule 2002; gastropods, Myers and Southgate 1980). These differences may reflect structural differences in the artificial substrata, geographical differences in study area, or the species composition of the communities. Irrespective, it should be noted that the mechanisms operating in our community may be different to those in similar macrofauna communities elsewhere.

2.5.3 Selection of univariate indices of community structure for monitoring assembly

While richness, evenness (J') and total abundance were all useful indices of change in community structure with assembly, Shannon-Wiener diversity (H') was not. This was because J' was negatively associated with richness, which occurred despite the mathematical dependence of J' on richness, at least for communities of less than 20-25 taxa (Sheldon 1969, Hulbert 1971, Alatalo 1981, Smith and Wilson 1996). We found that using richness and evenness indices separately was a more useful univariate approach to describing community assembly. Richness and evenness indices used in tandem provided useful information on the assembly process and were more highly correlated with multivariate patterns in community structure than any single index, or combination of indices, examined here.

2.5.4 Conclusions

Anderson et al. (2005b), found that holdfast fauna of *Ecklonia radiata* showed consistent patterns of biodiversity across large spatial scales in northeastern New Zealand, and our results on temporal variation in southeastern Tasmania using artificial substrata show similarly consistent patterns. While 'development time' was important in determining community structure, communities, converged to a broadly similar community structure. These results are by-and-large encouraging for the use of artificial habitats for the exploration of macrofauna community dynamics and environmental monitoring. However, careful consideration of timing is required, since the results also suggest that these 'aggregations' of

organisms form structured communities (*sensu* Underwood 1986). While very short time intervals provide information on temporal variation in dispersal or recruitment to bare space, deploying habitats over periods greater than 5 months will result in communities that are more likely to reflect the structure and dynamics of communities established in natural substrata.

3 COMMUNITY ASSEMBLY IN MARINE MACROFAUNA COMMUNITIES I. TEMPORAL CHANGE IN THE RELATIVE ROLES OF RECRUITMENT AND SPECIES INTERACTIONS.

3.1 Abstract

Both pre- and post-settlement processes can be important in structuring marine communities. The recruit-adult hypothesis asserts that the relative importance of the two processes should depend on the abundance of settling individuals. The usual approach to examine this tenet is to compare among sites of varying rates of recruitment, but the relative importance of the two processes in structuring population and community composition may also vary temporally within a single site. We contrast the relative importance of recruitment and post-settlement species interactions in macrofauna communities of different age developed in artificial kelp holdfasts. We hypothesise that recruitment should be more important in determining community structure in young communities than in older ones because competition for resources is likely to be more intense in an established community and because an established community may inhibit or facilitate settlement and subsequent recruitment. For a given aged community, the relative importance of recruitment should also vary seasonally with changes in the abundance of potential recruits. To test the relative importance of recruitment and species interactions in structuring macrofauna communities of different age and season, holdfast communities obtained from a known deployment period were compared to predicted communities based entirely on the accumulation of monthly recruits across the same deployment period. Recruitment did influence kelp holdfast community structure, but its importance decreased as the communities aged and as the rate of recruitment increased. The actual communities were significantly different from, and significantly more variable than, the predicted communities. Richness was lower than expected from accumulation of recruits, suggesting the importance of competitive and/or

predatory interactions either between the established community and potential new recruits or among members of the established community (post-recruitment interactions). However, results were taxon specific, with evidence of recruitment-driven population dynamics (*e.g.* hiatellid bivalves), facilitation (*e.g.* serpulid polychaetes) and competition/predation (*e.g.* phyllodocid polychaetes), among the 100 families examined.

3.2 Introduction

It is widely understood that both settlement (*e.g.* Keough 1984, Gaines and Roughgarden 1985, Sutherland 1990, Booth and Brosnan 1995, Caley et al. 1996) and post-settlement processes (particularly competition and predation; *e.g.* Connell 1961, Underwood et al. 1983, Young and Gotelli 1988, Minchinton and Scheibling 1991, Edgar 1993, Benedetti-Cecchi 2001) are important in structuring marine communities. Under the recruit-adult hypothesis (Menge 2000), their relative importance depends on larval supply (Gaines and Roughgarden 1985, Connolly and Roughgarden 1999b, Connolly et al. 2001). When settlement rates are low, space and other resources are available for all potential recruits, and so pre-settlement processes have a large influence on community structure. However, when settlement is high, crowding can lead to competition among resident species, or resident species may facilitate (*e.g.* Minchinton 1997) or inhibit recruitment of new individuals (of other species or con-specifics) through a variety of mechanisms (*e.g.* Levin 1982, Dahms et al. 2004, Dunstan and Johnson 2004), providing the frequency and intensity of disturbance is not too great (Dial and Roughgarden 1998). In these circumstances, post-settlement interactions most strongly determine community

structure. This has been well demonstrated in sessile intertidal communities where local and regional differences in population dynamics has been explained largely by spatial variation in settlement and the relative importance of pre- and post-settlement processes (*e.g.* Gaines and Roughgarden 1985, Minchinton and Scheibling 1991).

Whether these processes influence the dynamics of other marine macrofauna communities in a similar manner is less well established. We examined the relative importance of recruitment and post-settlement interactions in macrofauna communities established in artificial kelp holdfasts. The analysis could be approached in two ways, either focusing on the contribution of post-settlement interactions or on the contribution of larval supply/recruitment to community structure and variability. Both approaches have limitations.

A focus on post-settlement interactions, which typically attempts to document the nature and strength of post-settlement interactions, is difficult to apply in speciose marine communities (Underwood et al. 1983). Interactions can be weak in speciose communities (Kokkoris et al. 1999) and variability in larval supply may mask species interactions by influencing the power of statistical analyses (Young and Gotelli 1988). Furthermore, traditional methods of testing for interactions such as interspecific competition in complex natural communities are fraught with difficulty. For example, non-random species co-occurrence patterns can be explained by neutral processes (Ulrich 2004, Bell 2005), niche overlap can be used as evidence for or against the presence of competition (Sale 1974), and microcosm or lab-based experiments may be unrealistically simplistic for speciose communities because interactions may be non-linear,

density dependent, or influenced by a raft of other external factors (Underwood et al. 1983). Also the number and complexity of indirect interactions is unlikely to be fully resolvable for most real communities (Johnson and Seinen 2002).

Because of these limitations, most studies focus on determining the relative influence of larval supply/settlement on community structure (*e.g.* Gaines and Roughgarden 1985, Minchinton and Scheibling 1991). However, one issue with this type of approach is that recruitment is used as an index of larval supply or settlement. This is problematic because the relationship between larval supply, settlement and recruitment may vary among sites with variation in the presence of morphogenic cues for settlement, and through variation in immediate post-settlement mortality (Underwood and Petraitis 1993, Connolly et al. 2001). Another potential problem is that the timing of larval supply varies among sites (*e.g.* Menge 1991), confounding any focus on the spatial differences in larval supply. Avoiding these problems is difficult because direct measurement of larval abundance in the water column will include individuals that are not competent for settlement (Caley et al. 1996), and because settlement is difficult to estimate unless the larval period is clearly circumscribed and short, or larvae are sufficiently large to allow direct observation in the field (*e.g.* Stoner 1990), or sampling is very frequent (*e.g.* Connell 1985, Gaines and Roughgarden 1985).

One approach to determine the role of recruitment while avoiding issues of confounding larval supply among sites with variation in larval settlement cues or variation in the timing of settlement, is to examine the importance of recruitment within a single site, in identical habitats, across different aged communities and

seasons. While approaches examining the relative influence of recruitment and post-settlement interactions typically compare population and community dynamics among sites with varying settler abundance, the relative importance of these two classes of process may vary temporally within a single site. The history of arriving individuals may have a larger influence on younger patches where space and other resources are more available, while in longer established patches resident species are more likely to interact with each other and any potential new recruits. While this emphasises the need to consider community age when examining settlement/recruitment and species interactions, it also allows for comparison of the relative importance of these two processes, because the source of recruits and any morphogenic settlement cues are likely to be consistent across treatment groups (Connell 1985).

We examined the relative importance of recruitment and species interactions in structuring marine macrofauna communities by comparing communities establishing in artificial kelp holdfasts over 2-13 month deployments with predicted communities constructed by summing recruitment in artificial kelp holdfasts deployed successively for shorter time intervals (1 month) over the same time period. The experimental design was temporally hierarchical so that the effect of season on the importance of recruitment for each community age could be considered. This is important because recruitment and the outcomes of species interactions may vary with seasonal changes in the supply of recruits (Booth and Brosnan 1995). We studied the communities that established in artificial kelp holdfasts because we could control the time of instigation and age of the community. Based on current theory, differences in community structure between actual communities and predicted communities should be lowest in

younger communities than in older ones, and for a given community age, during times of low rather than high rates of recruitment. However, differences between actual and predicted communities should increase with community age and/or with an increase in the rate of recruitment (*e.g.* through seasonal variation). While overall patterns are likely to suggest that competition becomes increasingly important as communities become crowded, facilitation can also be an important mechanism for inducing settlement and/or metamorphosis in many marine organisms (Crisp 1974, Pawlik 1992). Thus, individual species may behave differently to the broad patterns observed at the community level.

The objectives of this study were to: (1) test whether community structure varied between communities established in artificial kelp holdfasts of varying age and season of deployment and those predicted solely on the basis of recruitment into 'fresh' uninhabited holdfasts; (2) examine the nature of differences in community structure between actual communities and predicted communities; and (3) examine whether the patterns observed at the community level were reflected by individual families.

3.3 Materials and Methods

3.3.1 Experimental design and field work

Artificial kelp holdfasts (hereafter 'holdfasts') were of similar size and physical complexity to the holdfasts of *Ecklonia radiata*, the most common species of kelp in southern Australia. Holdfasts were deployed to concrete supports set out on a grid over sand adjacent to a healthy *E. radiata* dominated reef in the

Derwent River Estuary, Tasmania, Australia (42° 57.7' S, 147° 20.5 E). Holdfasts were deployed each month for 13 months beginning in December 1997. At each deployment, sufficient holdfasts were established to collect 6 replicates each subsequent month until January 1999. Due to poor weather, holdfasts were neither collected nor deployed in September, while collections were not possible in June. For treatments deployed in December 1997, 4 replicates (rather than 6) were collected each subsequent month. Thus, a total of 408 holdfasts were deployed to, and recovered from, random positions on the grid. Further details on the experimental design and construction of holdfasts are described in Chapter 1.

Solitary animals retained on a 1mm sieve were identified where possible to the level of family, the most notable exception being amphipods, which were identified to sub-order. Colonial organisms were not enumerated because they were very rare. We deemed taxonomic resolution to the level of family as the optimal cost-benefit trade-off given the large abundance of organisms encountered (148,841 individuals), and that family-level patterns typically reflect patterns at the species-level (Williams and Gaston 1994, Faith et al. 1995, James et al. 1995, Somerfield and Clarke 1995, Balmford et al. 1996, Olsgard et al. 1997, Mistri and Rossi 2001, Dahl and Dahl 2002, Olsgard et al. 2003, Anderson et al. 2005a, Anderson et al. 2005b).

3.3.2 Estimating recruitment

Holdfast communities 1 month in age and deployed in each month of the experiment (December 1997-January 1999) were used to estimate the monthly recruitment of each family. This definition of recruitment incorporates some of

the impacts of post-settlement interactions between individuals, such as predation on early life-stages (Osman and Whitlach 1995c, b, Osman and Whitlatch 1996). The effect of including immediate post-settlement interactions means that conclusions on the relative importance of interactions over recruitment are more conservative. Note that recruits could arise from settling larvae or through migrating adults, although migration of adults was intentionally limited through the isolation of holdfasts on the sand substratum.

3.3.3 Testing the importance of recruitment

To test the relative importance of recruitment and species interactions in structuring macrofauna communities of different ages, holdfast communities obtained from a known deployment period (hereafter 'actual communities') were compared to 'predicted' communities based entirely on the accumulation of recruits across the same deployment period. If recruitment is important in structuring these communities then the actual community for a given time period should be similar to that predicted from recruitment over the same time period. If recruitment is less important than the interactions that occur between individuals within a kelp holdfast, then actual communities should appear more and more dissimilar to predicted communities as community age increases.

Predicted communities were constructed for each deployment period (*i.e.* each combination of date of deployment and community age) by randomly selecting a single holdfast community (from 6 replicates) from each month of the deployment period. The abundance of each family was then summed across the holdfast communities selected. The process was repeated until there were 15 predicted communities for each deployment period. Individual holdfasts could be

selected more than once in different predicted communities, but a predicted community was rejected if it was made up of the exact same combination of holdfasts as that of previously constructed predicted community. Note that the analysis was also conducted by summing the average holdfast communities (*i.e.* average of the 6 replicates for each 1-month deployment) for each month of the total deployment period; however, the results were similar and so are not presented.

Communities (actual and predicted) encompassing time periods that overlapped with any of the missing 1-month time intervals (May-June 1998, August-September 1998 and September- October 1998; see 'Experimental design and field work') were either excluded from the analysis (if community age was ≤ 3 months) or the missing 1-month time intervals in the predicted communities were estimated from or replaced with a 2-month time interval. Specifically, recruitment for the time interval of August-October 1998 was estimated using 2-month old communities rather than two separate sets of 1-month old communities, and recruitment from May–June 1998 was estimated by subtracting the average community for the deployment period June-July 1998 from the average community for the deployment period May-July 1998 (negative values were converted to zero). This meant that there was a single 'replicate' of recruitment for the time interval May-June 1998. These decisions were based on an initial interpretation of results which showed that the magnitude of difference between actual and predicted communities were the lowest for communities of 2-months in age (although still statistically significant). The influence of these necessary substitutions was to make

conclusions on the relative importance of interactions among species over recruitment more conservative.

3.3.4 Analysis

Univariate and multivariate techniques were used to compare actual holdfast communities to those predicted by summing recruitment for 1-month time intervals. Three univariate metrics were used to describe differences in community structure between actual and predicted communities: familial richness (total number of families), total abundance and Pielou's evenness, J' (Pielou 1966, 1969). To examine the influence of changes in seasonal rates of recruitment we plotted the difference in richness between actual and predicted communities against the average richness of recruits per month.

For the multivariate analysis we used Bray-Curtis similarity (Bray and Curtis 1957), after standardising abundances and performing fourth-root transformations to prevent abundant species from dominating the analysis (Clarke and Green 1988, Cao et al. 1998). Standardising the data allowed us to compare community structures using relative abundances of taxa rather than absolute abundances of taxa. We also calculated Bray-Curtis similarities on the unstandardised (and fourth-root transformed) data to compare actual and predicted communities in terms of differences in abundance and community structure. Non-metric multi-dimensional scaling (nMDS) plots were used to graphically represent patterns in Bray-Curtis space. Analysis of similarities (ANOSIM; Clarke and Green 1988) was used to test for differences in mean community structure and/or the spread of communities in Bray-Curtis space between actual and predicted communities. Multivariate dispersion was used to

examine the spread of communities in Bray-Curtis space and so was useful in interpreting significant ANOSIM results. Multivariate dispersion is defined as the sum of the squared distances (dissimilarity) from each replicate observation to the group's centroid (Anderson 2001). This value cannot be calculated directly in Bray-Curtis space, but can be determined indirectly because it is equivalent to the sum of the squared Bray-Curtis distances among replicate observations divided by the number of replicates (Anderson 2001). Because sample sizes varied between actual and predicted communities (6 and 15 respectively), we present average multivariate dispersion, by dividing sum of the squared distances from each replicate observation to the group's centroid by the number of replicates. Plots presented display this average multivariate dispersion, averaged across the different deployment dates, and so standard error bars presented represent experimental error and seasonal variability in dispersion. Paired 2-tailed, *t*-tests were used to identify whether actual communities were significantly more or less disperse than predicted communities.

Overall results suggested that species interactions play an important part in structuring these macrofauna communities in that there were, on average, more families and individuals in the communities estimated by accumulated recruitment than in the actual communities. However, analyses conducted on the abundances of individual families indicated that this trend did not hold for all families. To illustrate the diversity of trends, we present the change in abundance of three common families with community age for both actual and predicted communities. To objectively select these representative families a SIMPER (PRIMER5) analysis was performed for each community age (results are not presented; Clarke and Warwick 2001). We selected the families

Phyllodicidae (errant polychaete), Serpulidae (sedentary polychaete) and Hiatellidae (bivalve) for further analysis because they were identified as the major contributors to the dissimilarity between predicted and actual communities in the majority of the SIMPER analyses.

3.4 Results

3.4.1 Variation between actual and predicted communities

Predicted communities differed significantly from actual communities, and these differences became more pronounced as the communities aged (Figures 1 and 2). While in young communities there was overlap of the actual and predicted communities in nMDS space, the degree of overlap reduced as communities aged, and by 5 months there was no overlap between the two community types (Figure 1). A similar analysis of the unstandardised data yielded a quantitatively similar result (Appendix 2).

While the structure of older actual and predicted communities were clearly separated in nMDS analyses (Figure 1), significant ANOSIM results (Figure 2) may also be caused by differences in the dispersion of replicate communities. Dispersion was calculated for actual and predicted communities of each community age. Actual communities were significantly more dispersed than predicted communities for all community ages (Figures 1 and 3, Table 1). This difference became clearer with community age because the degree of dispersion in the predicted communities decreased with community age. There was no relationship between dispersion and community age for actual communities (Figure 3).

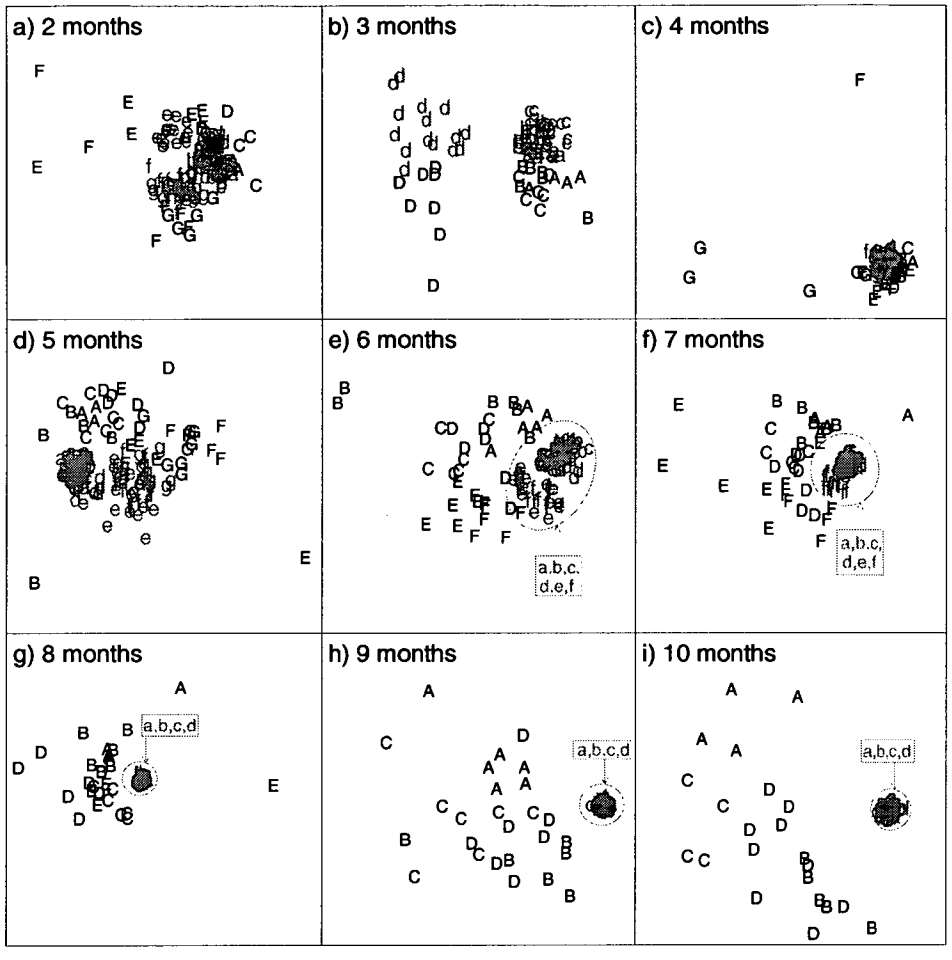

Figure 1 NMDS plots based on Bray-Curtis similarities (standardised and fourth-root transformed data) among actual holdfast communities (A-F, in black) and predicted communities (a-f, in grey) based on accumulated recruitment over successive 1-month time intervals, for the same community age. For a given nMDS, plot matching upper and lower case letters have the same deployment date and the sequence of letters represents the temporal sequence in deployment dates. Community ages were (a) 2 months (stress=0.19), (b) 3 months (stress=0.15), (c) 4 months (stress=0.17), (d) 5 months (stress=0.20), (e) 6 months (stress=0.16), (f) 7 months (stress=0.16), (g) 8 months (stress=0.11), (h) 9 months (stress=0.12), and (i) 10 months (stress=0.12).

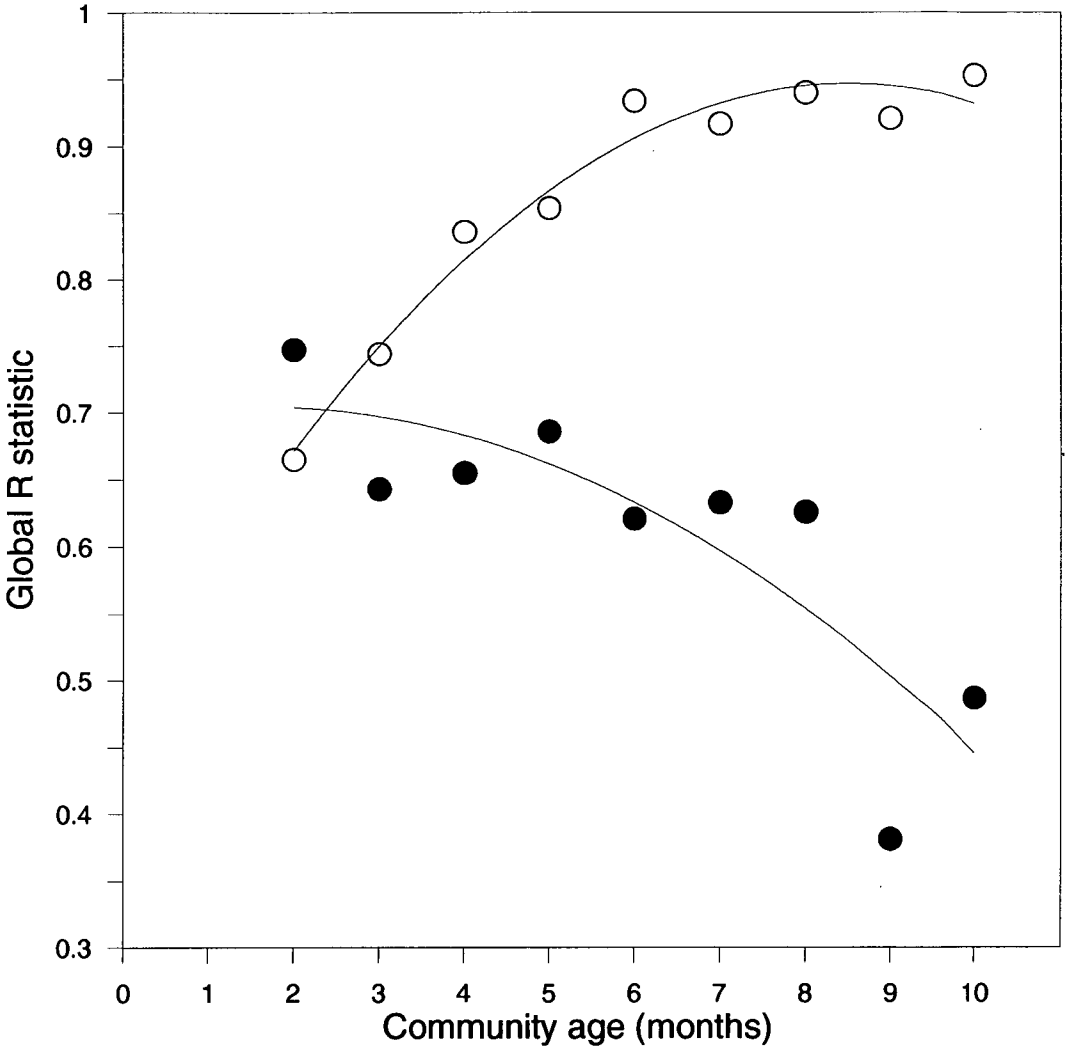

Figure 2 Change in the *Global R* statistic with community age (months), for each treatment in a 2-way ANOSIM. The statistic was used to test for significant differences between actual holdfast community structure and predicted community structure based on accumulated recruitment over 1-month time intervals (o), and to test the significance of differences in structure of actual communities of the same age but initiated on different deployment dates (•). All *Global R* values presented indicated a statistically significant effect of both community type and date of deployment ($P<0.0001$; based on 4999 permutations). Differences between predicted and actual communities increase with age and differences among communities initiated at different dates of deployment decrease with age? Data were standardised and fourth-root transformed before analysis.

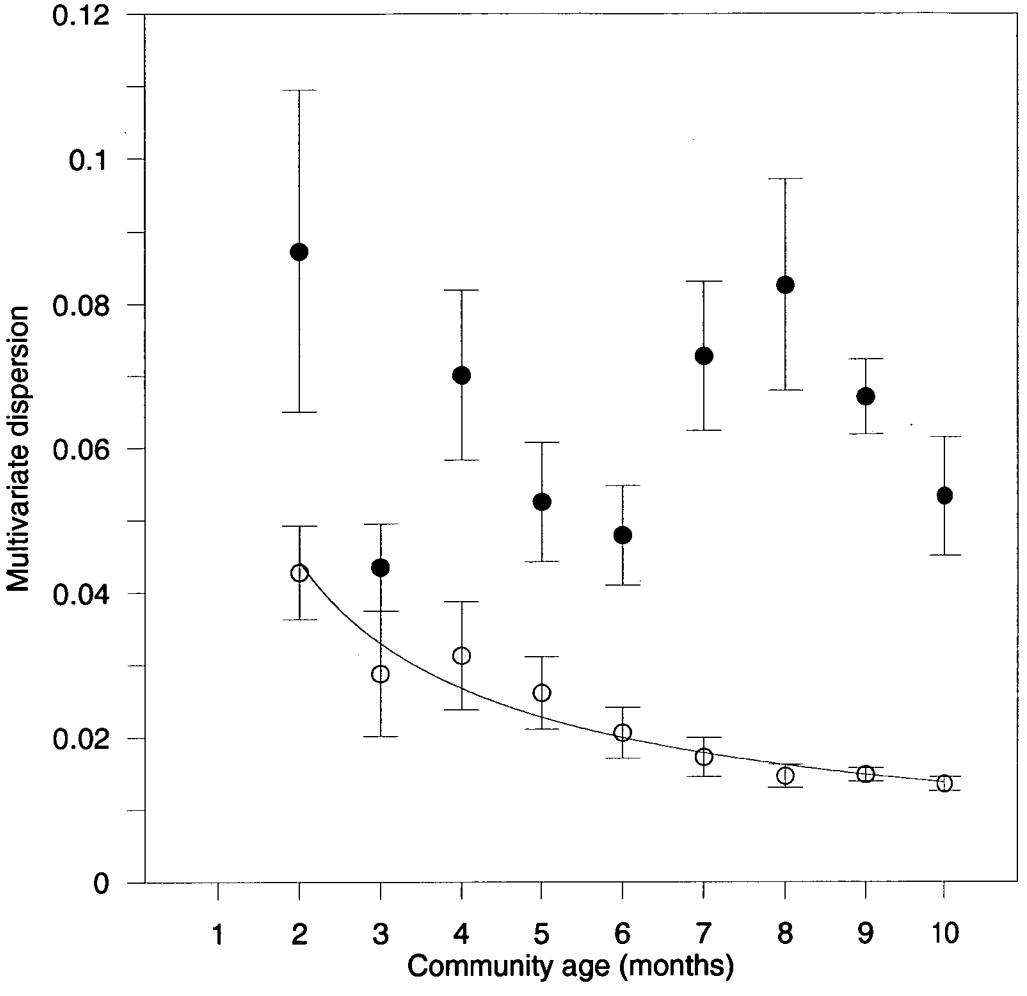

Figure 3 Change in multivariate dispersion (the average squared distance from replicate observations to the group centroid) of communities in Bray-Curtis space with community age. Data are for actual holdfast communities (•; y= -0.0003x + 0.07, P=0.88) and predicted communities based on accumulated recruitment over successive 1-month time intervals (o; Ln(y) = -0.72 Ln(x) - 2.60, P<0.0001, R^2 = 0.94). Dispersion values are averaged (±SE) across different deployment dates and hence the standard error contains components of experimental error and seasonal variability. Data were standardised and fourth-root transformed before analysis.

Table 1 Results of paired *t*-tests for each community age (months), testing the null hypothesis of no difference in the dispersion of the actual communities and predicted communities based on accumulated recruitment over successive 1-month time intervals (two-tailed). The tests were paired because replicate communities were obtained from different deployment dates. All results are significant at $P<0.05$. Note data were standardised and fourth-root transformed before calculation of dispersion.

Community age (months)	*d.f.*	*t* statistic	*P*
2	6	2.48	0.048
3	3	5.44	0.012
4	6	5.00	0.002
5	6	3.31	0.016
6	5	3.19	0.024
7	5	4.61	0.006
8	4	4.55	0.010
9	3	10.31	0.002
10	3	4.91	0.016

3.4.2 Variation in community structure

Richness, total abundance and evenness were used to illustrate how actual and predicted communities varied structurally. Richness was consistently higher in predicted communities than in actual communities, regardless of season, and this difference increased as the communities aged (Figure 4 and 5) and as the average richness of recruits per month increased (Figure 5). Differences in evenness were low between actual and predicted communities but did subtly reflect changes in the ratio of richness to total abundance in the predicted and actual communities (Figure 6). Total abundance on average showed a similar overall pattern to richness, however the point of divergence of actual and predicted communities occurred in older communities (Figure 7a). Differences in total abundance between actual and predicted communities were variable among the different deployment dates (Figures 7b-j).

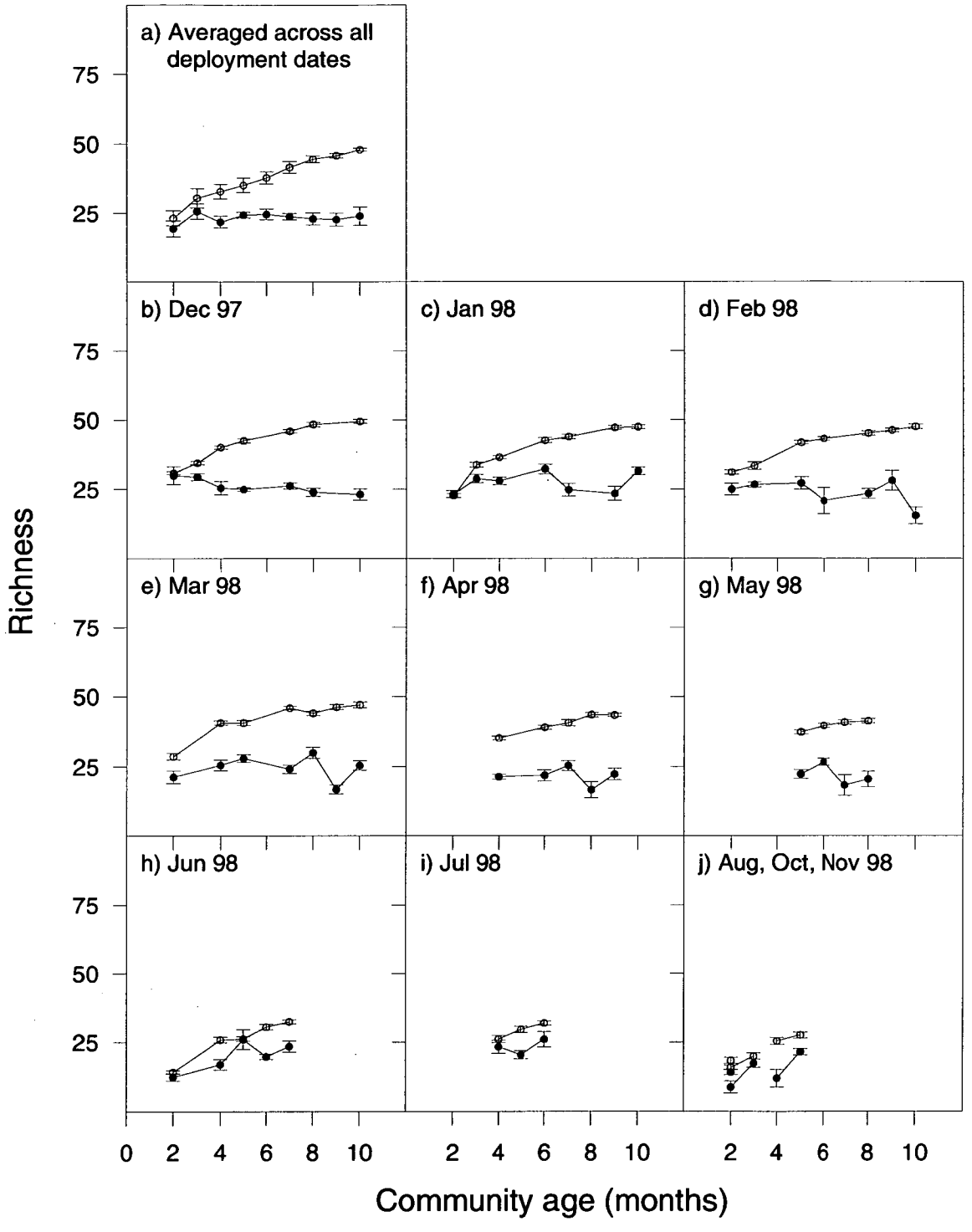

Figure 4 Change in richness (±SE) with community age in actual holdfast communities (•) and in predicted communities based on accumulated recruitment over successive 1-month time intervals (o), for each deployment date. Plots represent (a) the average across all deployment dates, and deployment dates of (b) December 1997, (c) January 1998, (d) February 1998, (e) March 1998, (f) April 1998, (g) May 1998, (h) June 1998, (i) July 1998 and (j) August-November 1998. Note that the number of replicates for communities deployed in December 1997 was 4 rather than 6.

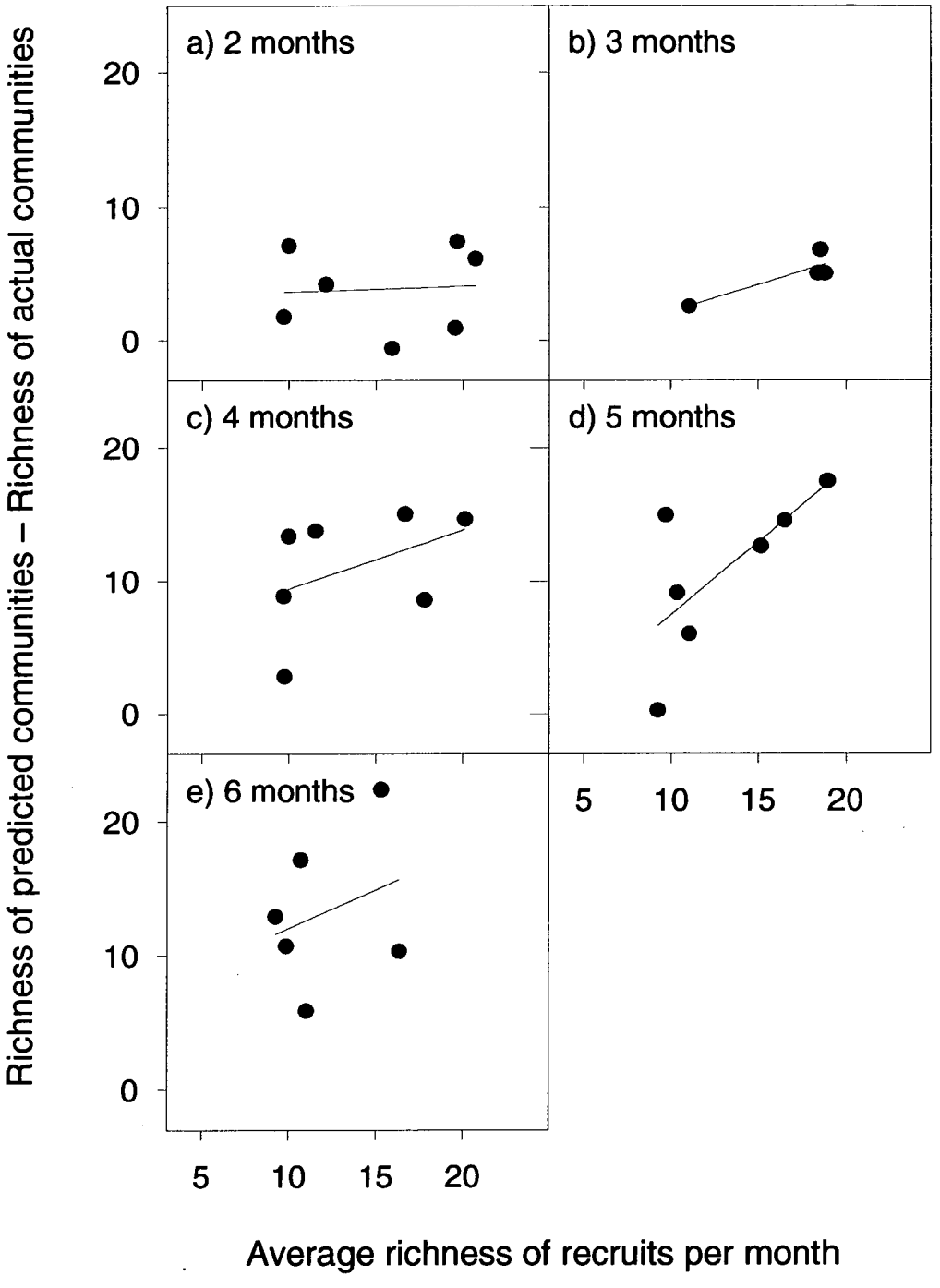

Figure 5 Relationship between the difference in richness of actual and predicted holdfast communities and the average richness of recruits per month, for different aged communities. Community ages were (a) 2 months, (b) 3 months, (c) 4 months, (d) 5 months and (e) 6 months. Older communities are not present because there were too few data points for meaningful interpretation. Trendlines are used to illustrate that the slope of this relationship is greater in older communities than younger communities.

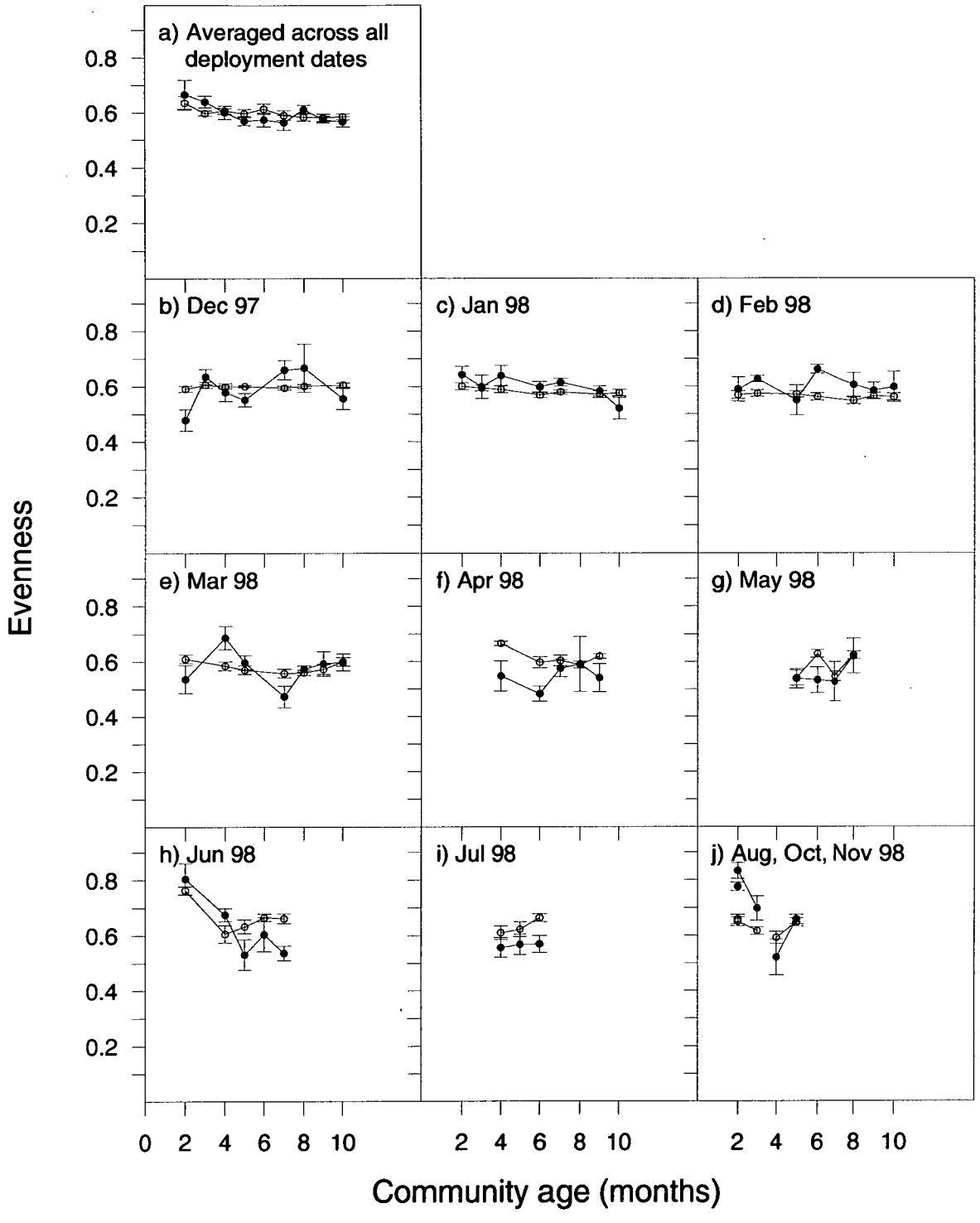

Figure 6 Change in evenness (J' ±SE) with community age in actual holdfast communities (•) and in predicted communities based on accumulated recruitment over successive 1-month time intervals (o), for each deployment date. Plots represent (a) the average across all deployment dates, and deployment dates of (b) December 1997, (c) January 1998, (d) February 1998, (e) March 1998, (f) April 1998, (g) May 1998, (h) June 1998, (i) July 1998 and (j) August-November 1998.

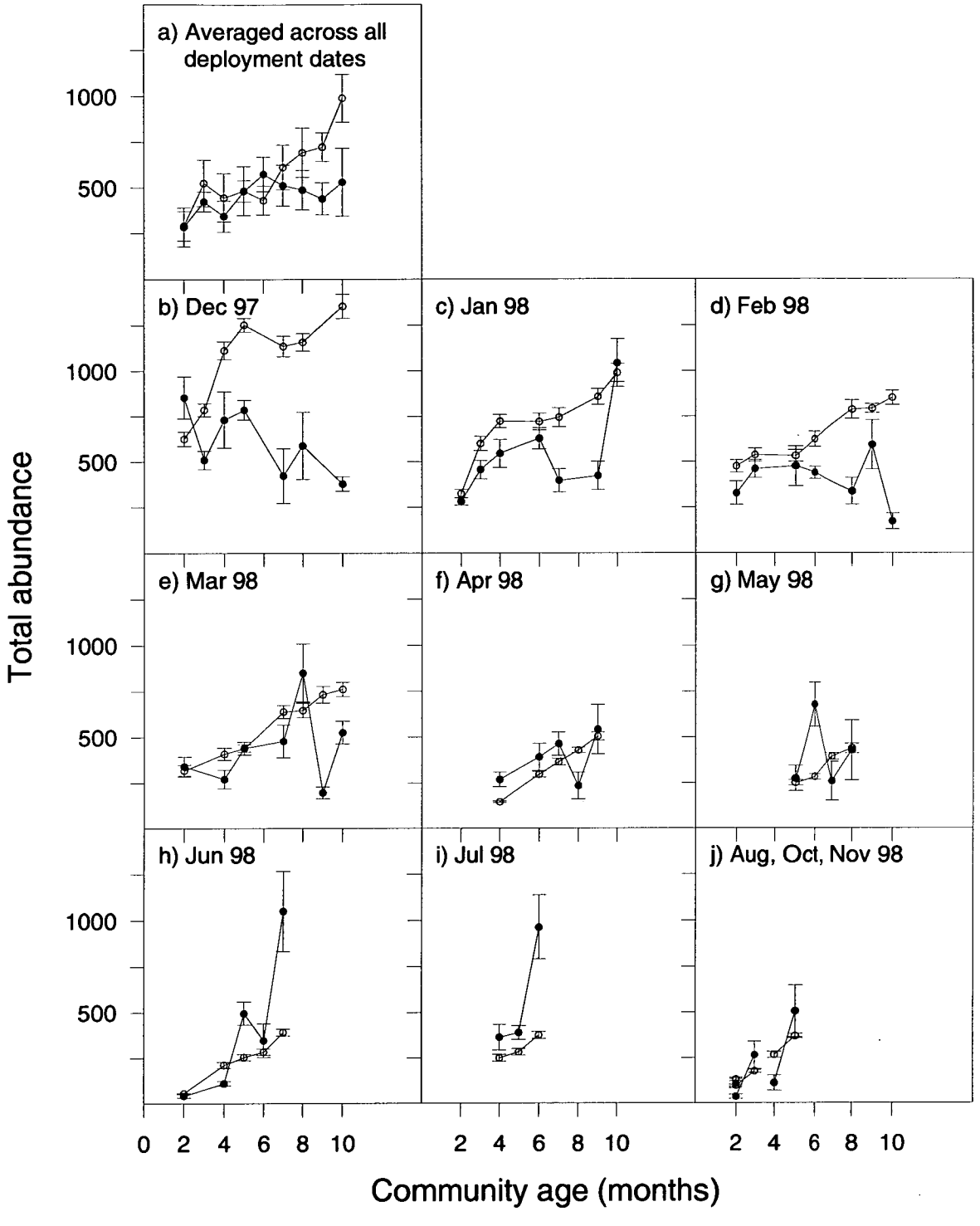

Figure 7 Change in total abundance (±SE) with community age in actual holdfast communities (•) and in predicted communities based on accumulated recruitment over successive 1-month time intervals (o), for each deployment date. Plots represent (a) the average across all deployment dates, and deployment dates of (b) December 1997, (c) January 1998, (d) February 1998, (e) March 1998, (f) April 1998, (g) May 1998, (h) June 1998, (i) July 1998 and (j) August-November 1998.

3.4.3 Variation at the family level

Variation in the abundance of the errant polychaete family Phyllodocidae between actual and predicted communities reflected community-level patterns in that there were fewer individuals in the actual communities than expected based on accumulation of recruits (Figure 8). In contrast, serpulid polychaetes were found in greater abundance in actual communities than in predicted communities (Figure 9), while there was no consistent pattern in the abundance of hiatellid bivalves (represented by a single species *Hiatella australis*) in the actual and predicted communities. On average there was little difference in the abundance of hiatellids between the actual and predicted communities (Figure 10a), however there were differences between predicted communities and actual communities for particular deployment dates. In December 1997, recruitment was extremely high and this level of recruitment also occurred in actual communities, since both actual and predicted communities had high abundances (Figure 10b). In January and February 1998, recruitment was higher in actual communities than in predicted communities (Figure 10c, d). For other deployment dates, recruitment was generally low and actual and predicted communities showed similar levels of abundance, unless the period of deployment was long enough to coincide with another peak in hiatellid recruitment in January 1999 (Figure 10e-j).

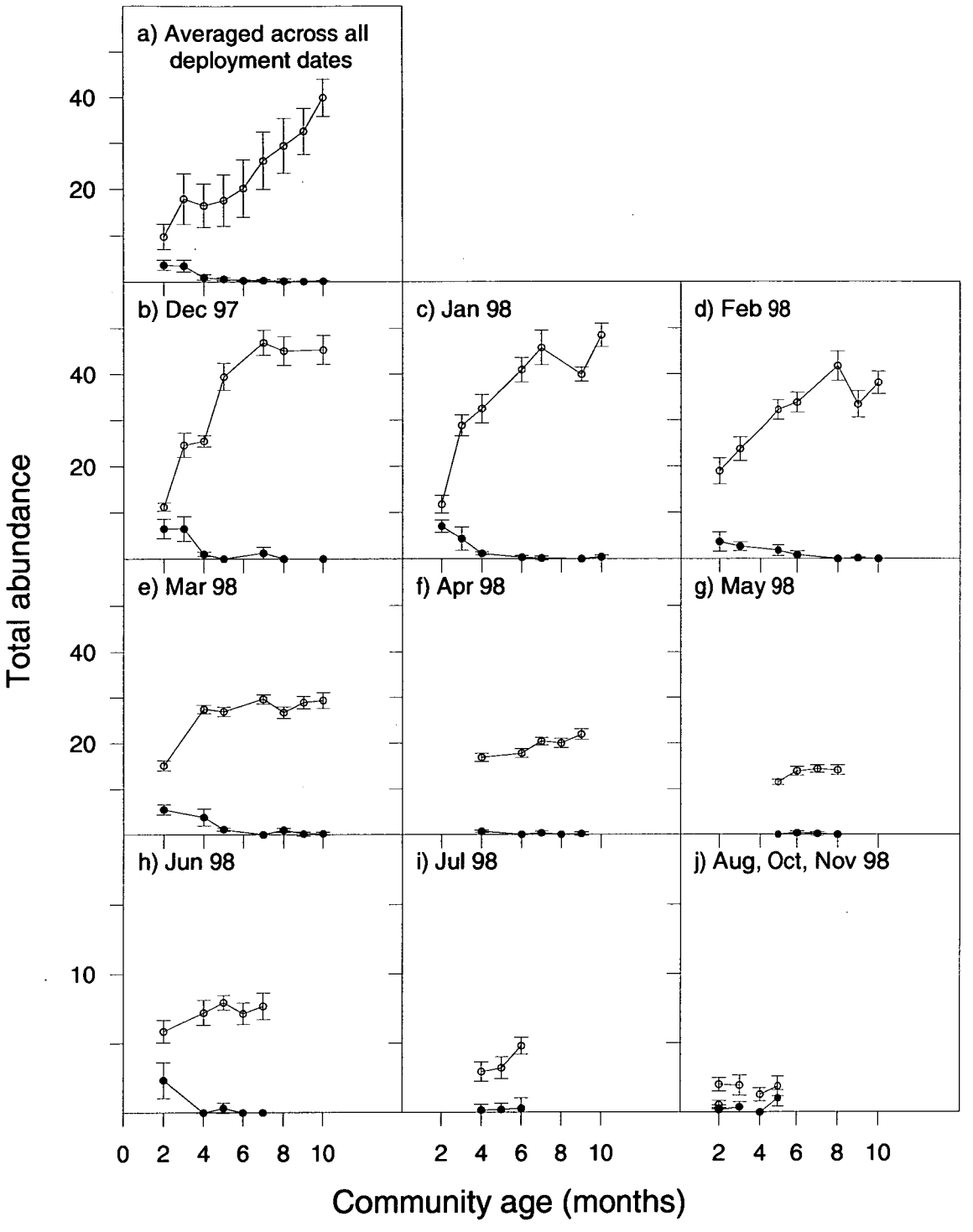

Figure 8 Change in the average total abundance (±SE) of phyllodocid polychaetes with community age in actual holdfast communities (•) and in predicted communities based on accumulated recruitment over successive 1-month time intervals (o), for each deployment date. Plots represent (a) the average across all deployment dates, and deployment dates of (b) December 1997, (c) January 1998, (d) February 1998, (e) March 1998, (f) April 1998, (g) May 1998, (h) June 1998, (i) July 1998 and (j) August-November 1998. Note changes in scale on the y-axis.

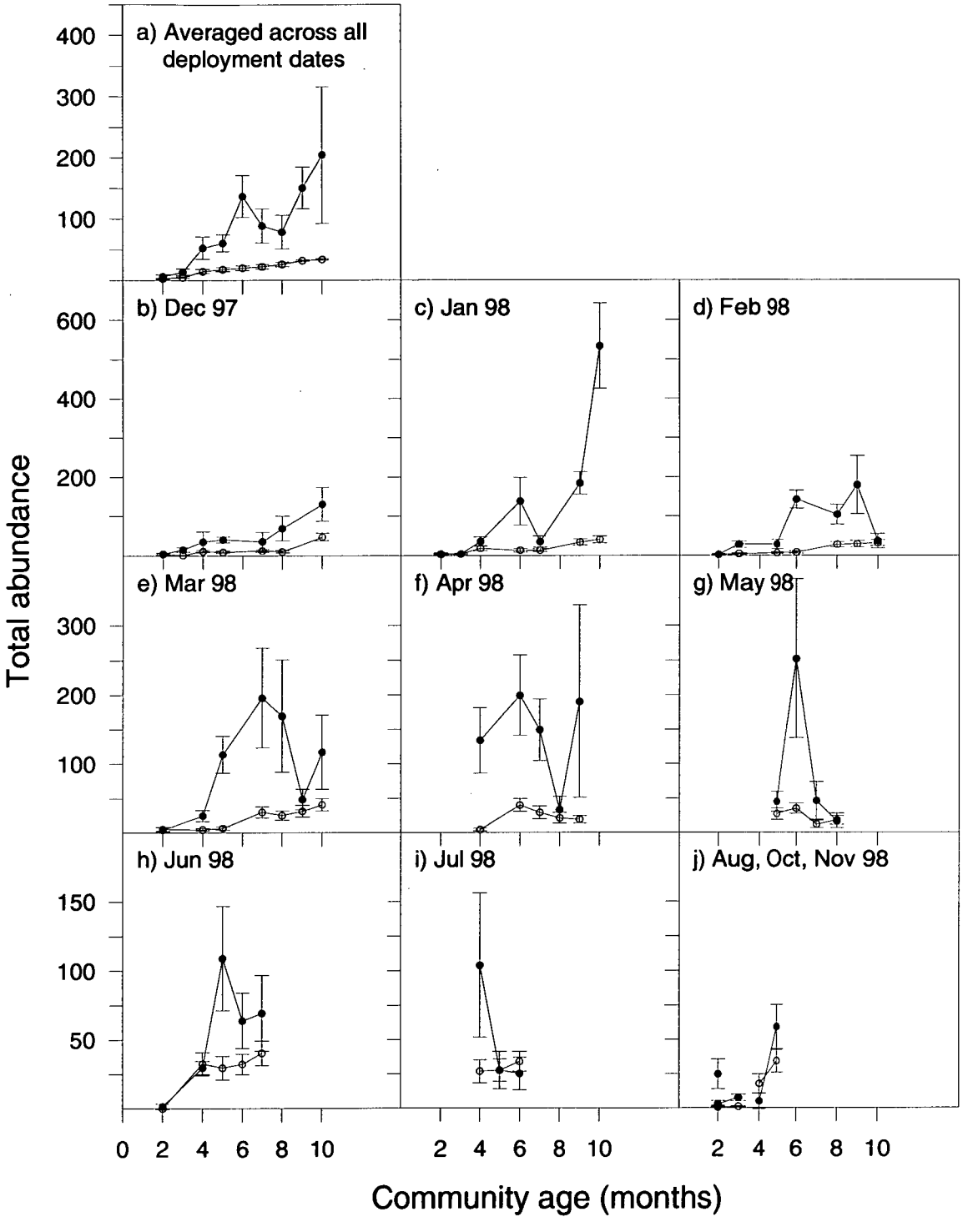

Figure 9 Change in the average total abundance (±SE) of serpulid polychaetes with community age in actual holdfast communities (•) and in predicted communities based on accumulated recruitment over successive 1-month time intervals (o), for each deployment date. Plots represent (a) the average across all deployment dates, and deployment dates of (b) December 1997, (c) January 1998, (d) February 1998, (e) March 1998, (f) April 1998, (g) May 1998, (h) June 1998, (i) July 1998 and (j) August-November 1998. Note changes in scale on the y-axis.

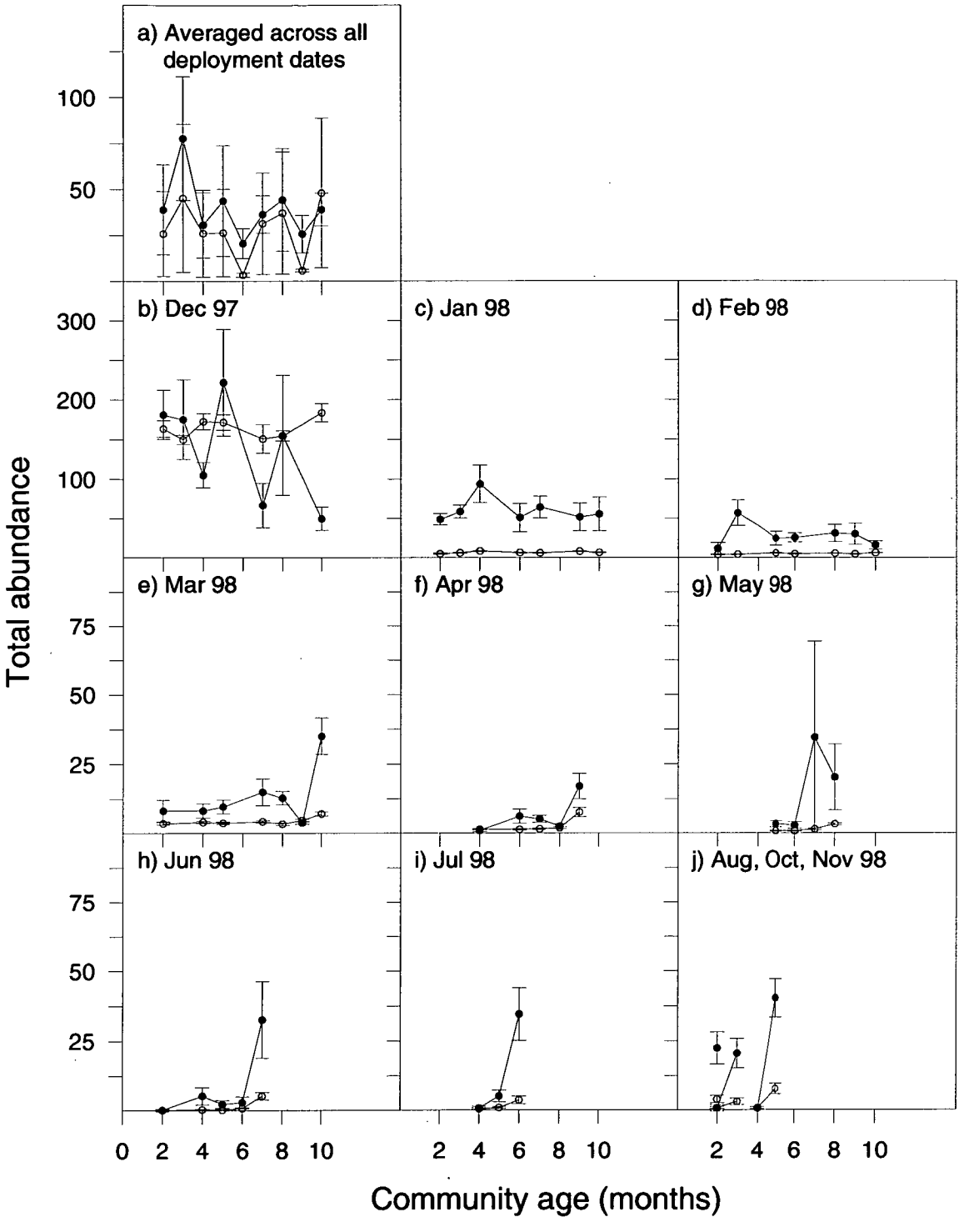

Figure 10 Change in average total abundance (±SE) of hiatellid bivalves with community age in actual holdfast communities (•) and in predicted communities based on accumulated recruitment over successive 1-month time intervals (o), for each deployment date. Plots represent (a) the average across all deployment dates, and deployment dates of (b) December 1997, (c) January 1998, (d) February 1998, (e) March 1998, (f) April 1998, (g) May 1998, (h) June 1998, (i) July 1998 and (j) August-November 1998. Note changes in scale on the y-axis.

3.5 Discussion

3.5.1 The influence of recruitment on community structure and dynamics

The relative influence of recruitment and species interactions have not been determined for marine macrofauna communities of varying age. We found that actual kelp holdfast macrofauna communities were significantly different from predicted communities based solely on the accumulation of monthly recruits. The magnitude of the difference between the actual communities and the predicted communities increased with age and with seasonal increases in the abundance of recruits. Actual communities contained fewer families and, more importantly, were significantly more variable. The difference in richness between the actual communities and those predicted from accumulation of recruits increased with community age, because richness reached a plateau in actual communities but continued to rise in the predicted communities. It seems unlikely that this simply reflected a carrying capacity on abundance in actual communities, since the total abundance of organisms was sometimes greater in actual communities than in predicted communities. The degree of variability (in Bray-Curtis space) among replicate actual communities was consistently high, while variability among replicate predicted communities decreased with community age.

There are a number of ecological processes that could potentially give rise to these patterns, including succession by replacement (Underwood and Chapman 2006), emigration caused by changes in habitat requirements of species during development, predation and competition. We could not identify any differences

in the abundance of families between young and old communities that could be explained by species replacements and succession in macrofauna communities is not generally thought to occur through species replacement (Ojeda and Santelices 1984, Dean and Connell 1987a, Edgar 1991a, Smith et al. 1996, although see Underwood and Chapman 2006). In addition transitory species that would only use a holdfast during an early stage of development were rare (a single individual rock lobster, 1 species of sea urchin and 2 species of fish). Thus, competition and predation which may be between members of the established community leading to mortality or emigration, or between the established community and potential recruits (pre or post-settlement species interactions), are the most likely processes.

3.5.2 Evidence of facilitative interactions

While the results for the community as a whole suggest that recruitment may be inhibited by the existing community, results for individual families varied. Serpulid polychaetes were more abundant in the actual communities than predicted by simple accumulation of recruits; thus, certain species within the community either had a positive effect on serpulid settlement and/or recruitment, or individuals of this family were able to reproduce rapidly within the community after recruitment. The most likely mechanism is that the larvae were attracted to conspecifics, since the dominant species *Galeolaria caespitosa* has a planktotrophic larvae (Marsden and Anderson 1981) known to be a gregarious settler (Minchinton 1997). The hiatellid bivalves displayed complex seasonal behaviours in recruitment that are difficult to interpret. During times of very high and very low recruitment (December and autumn-spring, respectively) there was little difference in their abundance between the actual communities

and the predicted communities. However, during collection and deployment dates in warmer months (January-February 1998 and January 1999), there were moderate levels of recruitment to established communities but not to substrata used as the basis to estimate predicted communities.

3.5.3 Mechanisms for competition in marine macrofauna communities

Competition is widely accepted as an important determinant of marine macrofaunal community structure (*e.g.* Costello and Myers 1996, Smith and Rule 2002), and it is the most likely cause of the differences observed between the actual and predicted communities, since the structure of a kelp holdfast provides protection from predation by large predators. If competition is the primary process limiting the influence of recruitment, then the two most likely mechanisms are competition for space and/or food resources. Both of these mechanisms could explain reduced richness in actual communities and the contrasting results observed in the abundance of serpulid polychaetes and bivalves of the family Hiatellidae. While space may be limited for species confined within the holdfast, sessile species can create their own space by aggregating on the outer surface of the holdfast. Both the hiatellid bivalves and the serpulid polychaetes are suspension feeders and so are also less reliant on production occurring within the holdfast.

The variable patterns in total abundances are more difficult to interpret. Total abundance was certainly lower in many actual communities compared to predicted communities, but some actual communities (particularly those collected in January 1999) supported very large numbers of organisms,

predominately crustaceans (Chapter 2). This suggests that space and food were not limiting in holdfasts collected on this date, unless the community was only temporarily swamped and any 'correction' to abundances hadn't yet had time to have an effect. Unfortunately, the experiment ended in January 1999 and so the persistence stability of these communities could not be determined.

3.5.4 Sources of variability in marine macrofauna communities

Results showing that actual macrofauna community structure was more variable than that of predicted communities based on accumulation of recruits were surprising given that recruitment is generally thought to increase variability in community dynamics through variation in larval supply (Gaines and Bertness 1992, Navarrete et al. 2005). However, as successive 1-month-old communities were added together to create predicted communities, the dispersion among replicates decreased and month-to-month variability was smoothed out. Underwood and Chapman (2006) also reported this effect and found higher Bray-Curtis dissimilarities among replicate actual communities than among predicted communities. In intertidal and subtidal habitats, small-scale variability in community structure is often very high (*e.g.* Underwood 1996, Dunstan and Johnson 1998, Benedetti-Cecchi 2001, Coleman et al. 2002, Anderson et al. 2005a, Fraschetti et al. 2005) suggesting the relative importance of small-scale physical and biological interactions over larval supply in influencing community dynamics. Our results appear consistent with this observation. While our definition of recruitment incorporated both variability in larval supply and effects of immediate post-settlement interactions, these were insufficient to account for the level of variability seen in community structure in older communities. Note that the contribution of species interactions to community

variability may be direct or indirect. Species interactions *per se* may not have caused the variability observed in actual communities; instead these interactions (e.g. competition and predation) may increase the exposure of the community to a variable supply of recruits.

3.5.5 Conclusions

Recruitment is an important determinant of kelp holdfast community structure irrespective of community age, but it becomes less important in older communities where interactions between taxa significantly influence community structure and variability. Our conclusions are similar to those of others working on sessile communities (*e.g.* Gaines and Roughgarden 1985, Roughgarden et al. 1985, Sutherland 1990, Minchinton and Scheibling 1991, Connolly and Roughgarden 1999b, Menge 2000).

Interactions among species that influence community structure include the effects of the established community on recruitment success, and interactions among post-recruitment individuals in the established community. Organisms may recruit and mature but then subsequently emigrate or die as a result of competition or predation. We cannot separate these two processes except for the families Hiatellidae and Serpulidae which recruited in much larger numbers to established communities than to fresh and largely unoccupied habitats. Differences between actual and predicted communities may also have been driven by a simple carrying capacity on total abundance. In Chapter 4, a subset of this data is analysed using a series of models of varying ecological reality, to determine whether these results could have been caused by a carrying capacity

on abundance, and whether the primary interactions occur between adults or between the existing community and potential recruits.

4 COMMUNITY ASSEMBLY IN MARINE MACROFAUNA COMMUNITIES. II. THE NATURE OF SPECIES INTERACTIONS

4.1 Abstract

Current theory on the relative influence of recruitment and post-settlement interactions on the structure of marine communities suggest that post-settlement interactions are important in determining community structure and dynamics in benthic marine systems, particularly in crowded communities. However, it is not known whether the interactions among the established community (adult-adult interactions) or interactions occurring between the established community and potential recruits (recruit-adult interactions) have greater influence. Community assembly in macrofauna communities developed in artificial kelp holdfasts was monitored at 1-month intervals over a 12 month period. A series of null models based on monthly recruitment, and with increasing levels of ecological realism, were used to generate assembly trajectories based on different types of community dynamic. The assembly trajectory of these predicted communities was compared to the assembly trajectory of communities established in the field in an attempt to identify the important interactions shaping community dynamics. Recruitment was most important in younger communities but continued to play a role in older communities. However, the identity of recruits in established communities could not be accurately estimated from recruitment to bare space, highlighting the importance of recruit-adult interactions. There was evidence of both positive (facilitative) and negative recruit-adult interactions. Adult-adult interactions did not appear to have a large influence on community structure but did influence community variability. Taxa responsible for the difference between predicted and actual communities were either consistently overestimated or underestimated by the null models, irrespective of community age. This suggests that with more detailed manipulative experimentation and modeling, it may be

possible to identify interactions among taxa that are consistent in direction throughout the process of assembly of this species-rich community.

4.2 Introduction

Community structure is usually thought to be determined by habitat structure, the supply of individuals and the interactions that occur among species. When habitat structure is fixed it is possible to examine the relative influence of supply and species interactions in determining community structure. For example, the relationship between local and regional species richness has been used to identify the relative importance of these processes in a variety of community types (see Srivastava 1999 for review). A significant departure from a linear relationship between regional and local diversity is interpreted as evidence of a saturated community in which species interactions have a significant influence on community structure (Srivastava 1999).

In marine communities, the availability of potential recruits determines the relative importance of recruitment and species interactions in determining community structure (Gaines and Roughgarden 1985, Roughgarden et al. 1988, Connolly and Roughgarden 1999a, Connolly et al. 2001, Chapter 3). Recruitment is used as an index of supply or settlement and is usually defined as the number of individuals that arrive in a community or population during a census period defined by the observer (Keough and Downes 1982). Of the species interactions that do occur, it is not known whether the most important interactions influencing community structure occur among members of the established community (adult-adult interactions) or between established individuals and potential recruits (recruit-adult interactions). Some authors suggest that recruit-

adult interactions are important in determining actual recruitment and therefore community structure (Underwood and Denley 1984). However, this type of interaction is difficult to test or control for in experimental studies because recruitment is measured after post-settlement interactions have begun to influence community structure. Keough and Downes (1982) noted that the importance of adult-adult interactions may have been overestimated in some studies because recruit-adult interactions have not been properly considered. In a 1996 review, Caley et al. observed that many studies assume that the established community does not influence settlement or post-settlement mortality, and Pawlik (1992) noted that it is often assumed that larvae do not have the potential to actively select or avoid settlement sites. These kinds of assumptions may be particularly problematic when bare substrata are utilized to obtain an index of recruitment. This is because it is assumed that different community structures (*e.g.* presence or absence of an established community) do not influence the relative abundance of recruiting species (*e.g.* Edgar 1991b). It may also be a problem when recruitment is used an index of supply (*e.g.* Menge 1991), because the ratio of recruitment to supply will change if pre- and post-settlement interactions vary with different community structures (*e.g.* Minchinton and Scheibling 1991).

The discrete communities inhabiting subtidal kelp holdfasts (artificial or natural) are relatively spatially and temporally predictable (Anderson et al. 2005b, Chapter 3) despite their high richness and total abundance of organisms. Compared with intertidal communities, they are relatively free from natural disturbances because they are less affected by physical disturbance (Smith et al. 1996) and the structure of the holdfast provides refuge from predation by large

roaming organisms such as fish and echinoderms. Thus, these communities may be excellent models for examining recruitment dynamics in communities of mobile species. In Chapter 3, we found that species interactions were important determinants of structure in these communities, particularly in older, more developed communities and during high rates of recruitment. Both positive and negative interactions occurred; however, negative interactions appeared predominant since species richness was higher in predicted communities based on accumulations of monthly recruitment to bare space resulting in greater diversity and total abundance than in actual communities of the same age. While the positive interactions we detected clearly indicated interactions between established individuals and potential settlers through facilitation of settlement (*e.g.* Crisp 1990, Minchinton 1997), negative interactions may have occurred between the established community and potential settlers or among members of the established community.

Negative recruit-adult interactions include inhibition of settlement through space pre-emption (*e.g.* Bertness 1989), the action of inhibitory chemicals (Pawlik 1992), direct physical irritation or interference, and direct predation of potential settlers (Osman and Whitlach 1995c, b, Osman and Whitlatch 1996, Dahms et al. 2004). Adult-adult interactions could arise given a finite limit to the total abundance of individuals that a holdfast can contain, leading to competition for resources and either mortality, forced emigration or predation (*e.g.* Sutherland 1990). In this chapter we use a subset of the original data analysed in Chapter 3 to examine the relative importance of these two broad types of interaction in determining macrofauna community structure in kelp holdfasts. The approach was to tease out the effects of the different types of interaction on community

structure using a series of recruitment-based null models of increasing ecological realism. The basic approach was similar for each model; communities established over short time intervals (1 month) were used to predict community structure in older communities (2-12 months). Communities of different age were used to examine how the influence of the different types of species interactions varied with community age. Our aims were: (1) to assess whether differences between actual communities and predicted communities arise through a simple carrying capacity on total abundance; (2) to assess whether the order of arrival of species was a significant determinant of community structure; (3) to separate the effects on community structure of mortality and emigration (which arise through interactions among established adults) from those that arise through interactions between adults and potential recruits (*e.g.* facilitation, inhibition, interference, predation); and (4) to identify individual families that showed any consistency in the direction of their interactions with the established community. Assembly over the 12 months was examined because the effects of an increased rate of recruitment can be simulated by increasing the age of the community in the absence of disturbance. In both scenarios the community becomes more crowded and individuals are more likely to influence each other's behaviour and mortality. This study is important because pre- and post-settlement interactions may be more important in determining marine community structure than current approaches to studying marine community dynamics account for (Caley et al. 1996).

4.3 Methods

4.3.1 Collection of empirical data ('actual' communities)

Artificial kelp holdfasts (hereafter 'holdfasts') were of similar size and physical complexity to the holdfasts of *Ecklonia radiata*, the most common species of kelp in southern Australia. Holdfasts were deployed over sand within 5 m of a reef in the Derwent River Estuary, Tasmania, Australia (42° 57.7' S, 147° 20.5 E), in January 1998. A sufficient number of holdfasts were deployed so that 6 replicates could be collected each subsequent month until January 1999. Due to poor weather, holdfasts could not be collected in June and September. Thus, a total of 60 holdfasts were deployed to, and recovered from, randomly selected positions. For brevity, these communities are termed 'actual' communities.

Solitary animals retained on a 1 mm sieve were identified where possible to the level of family, the most notable exception being amphipods, which were identified to sub-order. Colonial organisms were not enumerated because they were very rare. We deemed taxonomic resolution to the level of family as the optimal cost-benefit trade-off given the large abundance of organisms encountered (27,090 individuals in this part of a much larger experiment), and that family-level patterns typically reflect patterns at the species-level (Williams and Gaston 1994, Faith et al. 1995, James et al. 1995, Somerfield and Clarke 1995, Balmford et al. 1996, Olsgard et al. 1997, Mistri and Rossi 2001, Dahl and Dahl 2002, Olsgard et al. 2003, Anderson et al. 2005a, Anderson et al. 2005b).

4.3.2 Estimating recruitment

Holdfast communities 1 month in age and deployed as 'fresh' uninhabited holdfasts each month of the experiment (December 1997-January 1999) were used to estimate monthly recruitment of each family. This definition of recruitment may include impacts of immediate post-settlement interactions between individuals (Keough and Downes 1982). The effect of including possible early post-settlement interactions on our analysis was to make conclusions on the importance of species interactions over recruitment more conservative. Note that new recruits could be settling larvae or migrating adults, although migration of adults was intentionally limited through the isolation of holdfasts over sand.

4.3.3 Missing data

Due to poor weather, holdfasts could not be collected in June and September. Thus, communities of ages 5 and 8 months were not included in the analysis. For the recruitment data, 2-month-old holdfast communities were used to replace 2 successive 1-month-old holdfast communities where there was missing data (May-July and August-October). There was also a missing individual replicate for the collection date of November 1998 (10-month-old community). This holdfast community was replaced with the average of the 5 remaining replicate holdfasts (rounded to whole numbers). Maintaining the number of replicates at 6 was important because Model 2 communities (see below) were generated by random sampling from communities pooled across replicates and deployment dates.

4.3.4 Null model construction

Five different models were designed (Models 1-5), these are described in sections 4.3.4.1 - 4.3.4.5, a summary of each of these models is presented in Table 1. All model communities were constructed using monthly recruitment data. However, in Models 2-5 pooled replicate communities were sampled by a random sampling routine. The total abundance of all organisms in communities generated using Models 2-5 was set by the total abundance observed in an actual community of the same age. Actual communities were also used to set a net value for the combined effects of mortality and emigration of each family in Models 4 and 5. Mortality and emigration (hereafter 'mortality/emigration') are combined into a single value representing net decreases in population size of a family from one time interval to the next because it was not possible to separate these two effects. Note that our measure of mortality/emigration includes components of mortality due to senescence, predation, or any other interspecific interaction. The sampling routine used to select individuals in Models 2-5 occurred with replacement, thus we assumed that the relative abundance of each family in the pool of available recruits was constant. Note that while 4999 model runs (4999*6 replicate holdfasts) were generated for Models 2-5, to test for differences in dispersion among predicted and actual communities, a random subset of only 10 model runs (10*6 replicate holdfasts) were used for nMDS and ANOSIM analyses (see '*Statistical Analysis*').

Table 1 Summary of the attributes of each of the null models employed to construct model communities. Seasonality in recruitment was incorporated by using recruitment to 'fresh' unoccupied holdfasts in successive 1-month time intervals. 'Total abundance limited' refers to building model communities until the total abundance of organisms reaches that of a randomly selected actual community of the same age. Inhibition was simulated by allowing recruits into the community in the sequence they occurred in the monthly recruitment holdfasts, and imposing a carrying capacity determined from actual communities. Net mortality and emigration, as measured in actual communities, was modeled by either removing randomly selected individuals (Model 4) or those belonging to particular families identified by net reductions in actual communities (Model 5).

Null model	Seasonality in recruitment	Total abundance limited	Inhibition of further recruitment by early recruits	Mortality and emigration
Model 1	✓	✗	✗	✗
Model 2	✓	✓	✗	✗
Model 3	✓	✓	✓	✗
Model 4	✓	✓	✓	Random
Model 5	✓	✓	✓	Family specific

4.3.4.1 Null model 1

Model 1 communities were constructed simply by summing the monthly recruitment data for each family. A single replicate holdfast community was selected randomly from each successive 1-month time interval up to the required community age (2-12 months), and the final predicted community determined by summing the abundance of each family across all replicates selected. For example, a community labeled $C_{1,5}$ (deployed in the first month and collected in the fifth month) would be constructed by randomly selecting a replicate community from each of the following 1 month time intervals: $t_{1,2}$, $t_{2,3}$, $t_{3,4}$ and $t_{4,5}$. The process was repeated until there were 15 replicate Model 1 communities

for each community age. Model 1 communities incorporated seasonality in recruitment but did not incorporate any effects that early recruits might have on later recruits (these effects were allowed to occur in Models 4 and 5). The total number of individuals within the null community was unlimited and determined solely as the sum of the component monthly recruitments. Note that these were identical to the model communities developed in Chapter 3 and the approach to construction was similar to that in Underwood and Chapman (2006).

4.3.4.2 Null model 2

Model 2 communities of a given age (1-12 months) were constructed by summing recruitment across all 6 replicates and across each successive 1 month time interval, spanning the required deployment period. The relative abundances of taxa within the pool was assumed to reflect the relative abundances of taxa in the water column that were available to recruit over this time period (which cannot be measured directly). Individuals were then selected randomly from this pool, with replacement until the total number of individuals selected was the same as that observed in a single randomly selected replicate of an actual community of the same age. Selections occurred with replacements because in an open marine system the relative abundance of taxa within the water column is unlikely to vary with the recruitment of a relatively small number of individuals.

Like Model 1 communities, Model 2 communities incorporated seasonality in recruitment, and early and late recruits had the same likelihood of establishing. However, unlike Model 1 communities, the total number of individuals within each model community was limited by the number of individuals observed in an actual community of the same age. Thus, while Model 2 communities had a total

abundance that was either the same as or lower than the same aged Model 1 community, the relative abundance of each family was approximately the same.

4.3.4.3 Null model 3

Individuals were randomly selected from monthly recruitment data iteratively. In the first iteration, individuals were selected randomly from pooled replicates of the first 1 month time interval, until the total abundance was the same as that of a single replicate 1-month-old actual community. This was repeated for each of the 6 replicate 1-month-old communities (thus the first iteration was the same as that used to generate 1-month-old, Model 2 communities). In the second iteration, the total abundance of all organisms in each replicate of the model communities was increased until the total abundance was the same as a single replicate of an actual 2-month-old community (replicate communities were randomly paired). To do this, new individuals were selected randomly from pooled replicates of the second 1-month time interval. The iterations continued in this fashion until community age was equal to 12 months. Note that the routine for pairing replicates between time intervals was only semi-random since the routine rejected pairs that showed a decrease in total abundance from one time interval to the next, unless there was no other option and then rather than the removing individuals the total abundance of the model communities remained unchanged until the next iteration. The entire process was repeated 4999 times for each community age. Model 3 communities differed from Model 2 communities in that later recruits were prevented from entering the community once the carrying capacity was reached.

4.3.4.4 Null model 4

A similar iterative process used to build Model 3 communities was employed. However, before adding any new individuals to the model community at time *t* to form the model community at *t+1*, some individuals were removed to reflect observed net mortality/emigration in actual communities from time step *t* to *t+1*. The number of individuals removed at each step was calculated by summing the change in abundance of each family that decreased in abundance from the (randomly selected) replicate actual community used to set total abundance at *t*, to the (randomly selected) replicate actual community used to set total abundance at *t+1*. This number of individuals was then removed from the model community at *t* by randomly selecting individuals irrespective of their identity (family). New individuals were then added to the community, as described for Model 3, to construct the Model 4 community at *t+1*.

4.3.4.5 Null model 5

To construct a Model 5 community, the same iterative process used for Model 3 and 4 communities was employed, as was the method of calculating mortality/emigration described in Model 4. However, instead of removing individuals randomly from the each model community regardless of identity (as in Model 4), mortality/emigration was family specific. Familial abundances were reduced in model communities from time *t* to *t+1* by the same amount seen in actual communities from time *t* to *t+1*, unless there were fewer individuals in the predicted community than the number that needed to be removed, in which case the abundance of that family was reduced to zero.

4.3.5 Statistical Analysis

Univariate and multivariate techniques were used to compare actual holdfast communities to predicted communities generated with each null model. Three univariate metrics were used: familial richness (total number of families), total abundance and Pielou's evenness J' ($H'/log(S)$, Pielou 1966, 1969) where $H'=-\Sigma p_i \ln p_I$ (Margalef 1958), S= number of families in the community and p_i=proportion of total sample belonging to the i^{th} family. Average communities (actual communities n=6; Model 1 communities n=15; and Model 2-5 communities n=60) were used for each of the univariate metrics because this simplifies graphical output and allows for easier interpretation of the trajectory of assembly for each community type.

The multivariate analysis was conducted on both individual replicate communities (nMDS, ANOSIM, PCO and tests for variation in average dispersion) and on average communities (nMDS). All multivariate analyses were based on Bray-Curtis dissimilarities (Bray and Curtis 1957), calculated after data were fourth-root transformed to prevent numerically abundant species from dominating the analysis (Clarke and Green 1988, Cao et al. 1998). Non-metric multi-dimensional scaling (nMDS) plots were used to graphically represent patterns in Bray-Curtis space. On one occasion when stress values were high, Principal Coordinates Analysis (PCO; Anderson 2003) based on Bray-Curtis distances were used instead. Average Bray-Curtis dissimilarities between replicate actual communities and replicate model communities are also presented (SIMPER, PRIMER5; Clarke and Warwick 2001) in association with ANOSIM results.

1-way analysis of similarities (ANOSIM; Clarke and Green 1988) were used to test for differences in community structure among actual and predicted communities for each community age. Pair-wise *a posteriori* analyses were used to test whether model communities differed significantly from equivalent actual communities. *A posteriori* analyses conducted for each community age were corrected to control for the rate of Type 1 error using the sequential Bonferroni correction (Holm 1979, Quinn and Keough 2002).

Multivariate dispersion was used to examine the spread of communities in Bray-Curtis space and so was useful in interpreting significant ANOSIM results. Multivariate dispersion was defined as the average squared distance (dissimilarity) from each replicate observation to the group centroid, and was calculated by determining the sum of the squared distances and dividing by the number of replicates (Anderson 2001), and then dividing by the number of replicates again to find the average. Each of Models 2-5 was used to generate 4999 sets of 6 replicate holdfast communities, for each community age. These data were used to determine a distribution of average dispersion values (among 6 replicates) under each model community for each community age, which was then used to test whether actual communities were significantly more variable than equivalently-aged model communities. The test was one-tailed because a previous analysis (Chapter 3) showed that model communities underestimate the dispersion seen in natural communities. Model 1 communities could not be analysed in this way, because of the way they were constructed. Because of the way Model 2-5 communities were constructed, replicate observations of average dispersion could be generated; thus, in the graphical output, the means of

'average dispersion' for Models 2-5 are presented. Standard errors for these values of the mean of 'average dispersion' are not presented because they were essentially zero.

Results comparing Model 2 and Model 3 communities showed that communities 2-4 months in age generated by these models were not significantly different from each other. This was a little surprising given the differences in the way that these communities were constructed. This result could arise if monthly recruitment did not vary in the first 4 months of the experiment. To test this, PERMANOVA (Anderson 2001, McArdle and Anderson 2001) was used to test for differences in the structure of recruits each month, and where these results were significant, PERMDISP (Anderson 2004) was used to test for differences in dispersion of newly recruited communities among months. Pair-wise *a posteriori* tests were used to identify which months differed, and the sequential Bonferroni procedure was used to control for the rate of Type 1 error (Holm 1979, Quinn and Keough 2002). For the PERMANOVA, Monte Carlo *P*-values were used because the number of unique values of the test statistic were relatively low for each pair-wise comparison (Anderson 2005). Note that recruitment data based on 2-month-old time intervals (because of missing data) were not included in this analysis

A series of SIMPER analyses was used to identify whether model communities over- or under-estimated the abundance of individual families. SIMPER is used to identify those taxa that either contribute most to the average similarity within a treatment (i.e. between replicates) or to the average dissimilarity between two treatments (Clarke and Warwick 2001). We used SIMPER to identify families

that contributed most to the average dissimilarity between model and actual communities. Each SIMPER analysis was arbitrarily stopped once 40% of the dissimilarity between the model and actual community was accounted for; on average 14 families were selected for each comparison. Results for the 12 most frequently selected taxa (across all models and community ages) are presented.

4.4 Results

4.4.1 Behaviour of model communities

Total abundance, richness and evenness varied as the actual communities developed, while model communities varied in their ability to represent these patterns (Figure 1). Communities generated by Models 1-3 accumulated individuals and families through time and could not reflect decreases in total abundance or familial richness (Figure 1a and b). Models 4 and 5 by definition, had the same total abundance as that observed in the actual communities (Figure 1a), but did not accurately reflect the patterns in familial richness shown in the actual communities (Figure 1b). The accumulation of families in Model 5 communities was similar to that seen in Models 1-3 (Figure 1b). Notably, the number of families was over-estimated in these models compared to actual communities, and this difference increased in magnitude as the communities aged (Figure 1b). Model 4 communities poorly represented assembly in actual communities, since familial richness was usually underestimated and was highly variable through time (Figure 1b). Evenness, which was largely well predicted by the other model communities, was also underestimated and variable through time (Figure 1c).

4.4.2 Differences between actual and model communities

Predicted 1-month-old communities were not significantly different from actual 1-month-old communities. However, the structures of model communities >1 month in age were significantly different to those of the actual communities (Table 2). In most younger communities (except in 1-month-old communities) this appeared to be driven by differences in dispersion, and in older communities by differences in dispersion and/or community structure (Table 3, Figures 2 and 3). The distribution of replicate actual communities overlapped with the distribution of replicate model communities in multivariate space when the communities were young (Figure 2a and b) but not when they were older (Figure 2c and d). The largest differences in dispersion between actual and predicted communities were in Models 1-3, but these differences were also significant for Models 4 and 5 (Table 3; Figure 3). Differences in community structure between the model communities and actual communities became more pronounced as the communities aged. In particular, the trajectory of the average actual community diverged noticeably from the trajectories predicted by each model (Figure 4).

Average Bray-Curtis dissimilarities between actual and predicted communities provide some perspective on the scale of these differences. For communities of up to 3 months in age, average Bray-Curtis dissimilarities between actual communities and model communities ranged from 32.3% - 35.1% (Table 2; average=33.2%, standard error=0.3%). By the time communities were 10-12 months old, average Bray-Curtis dissimilarity between actual communities and model communities ranged from 37.0% - 60.3% (Table 2; average=49.8%, standard error=2.5%).

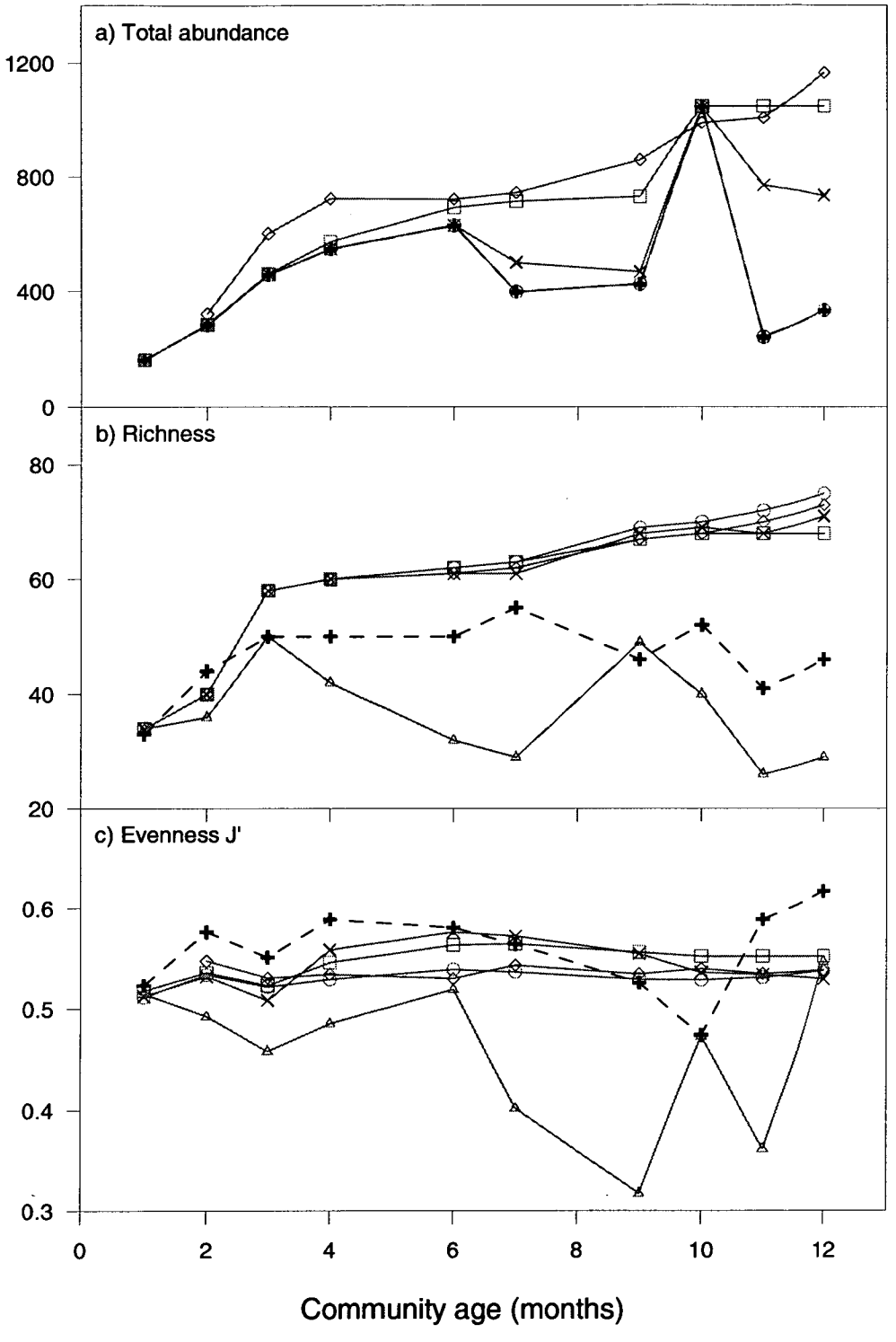

Figure 1 Change in a) total abundance, b) richness, and c) evenness of the average actual community (✚) and the average Model 1 (◇), Model 2 (○), Model 3 (□), Model 4 (Δ) and Model 5 (×) communities, with community age.

Table 2 Comparison of predicted communities to actual communities by community age. Presented is the average Bray-Curtis dissimilarity among replicate communities and the results of ANOSIM analyses comparing the structure of predicted and actual communities of each age for each model (*R* statistic [in bold] and associated significance for 4999 permutations). Data were fourth-root transformed before analysis. *P*-values were adjusted by the sequential Bonferroni correction to adjust for Type 1 error rate because all *a posteriori* comparisons are presented for interpretation (either here or in Table 4) for each community age, all *P*-values presented were significant at $P=0.05$. Note that for 1-month-old communities *P*-values are not presented, because the Global R value was not significant (*Global* $R=0.014$, $P=0.059$).

Average dissimilarity **R** (Significance of *R*)	Model 1	Model 2	Model 3	Model 4	Model 5
1 month	n/a	32.2 **0.37** (n/a)	32.0 **0.42** (n/a)	32.0 **0.46** (n/a)	31.7 **0.46** (n/a)
2 months	34.8 **0.56** (*P*<0.001)	32.6 **0.97** (*P*<0.001)	33.1 **0.90** (*P*<0.001)	35.1 **0.88** (*P*<0.001)	33.1 **0.87** (*P*<0.001)
3 months	32.3 **0.81** (*P*<0.001)	33.1 **0.91** (*P*<0.001)	33.6 **0.84** (*P*<0.001)	34.8 **0.55** (*P*=0.004)	32.4 **0.76** (*P*<0.001)
4 months	37.3 **0.95** (*P*<0.001)	37.5 **0.97** (*P*<0.001)	36.9 **0.97** (*P*<0.001)	39.4 **0.81** (*P*<0.001)	37.3 **0.86** (*P*<0.001)
6 months	34.7 **0.94** (*P*<0.001)	35.0 **1.0** (*P*<0.001)	35.7 **1.0** (*P*<0.001)	42.4 **0.99** (*P*<0.001)	40.1 **0.99** (*P*<0.001)
7 months	44.0 **0.89** (*P*<0.001)	43.5 **0.99** (*P*<0.001)	43.6 **0.99** (*P*<0.001)	54.2 **0.75** (*P*<0.001)	54.7 **0.94** (*P*<0.001)
9 months	48.5 **0.94** (*P*<0.001)	47.4 **0.88** (*P*<0.001)	49.4 **1.0** (*P*<0.001)	47.3 **0.54** (*P*=0.003)	57.6 **0.93** (*P*<0.001)
10 months	37.2 **0.98** (*P*<0.001)	37.0 **1.0** (*P*<0.001)	38.0 **1.0** (*P*<0.001)	48.1 **1.0** (*P*<0.001)	46.1 **1.0** (*P*<0.001)
11 months	68.3 **1.0** (*P*<0.001)	63.1 **0.99** (*P*<0.001)	57.5 **1.0** (*P*<0.001)	50.0 **0.67** (*P*<0.001)	56.8 **1.0** (*P*<0.001)
12 months	47.2 **0.98** (*P*<0.001)	42.0 **0.91** (*P*<0.001)	46.6 **1.0** (*P*<0.001)	48.1 **0.85** (*P*<0.001)	60.3 **1.0** (*P*<0.001)

Table 3 Results of randomization tests, testing whether model communities were less variable than actual communities. Presented is the average multivariate dispersion (in Bray-Curtis space) among replicate actual communities for each community age, the number of times average dispersion was greater than this value in 4999 permutations of each null model and the associated probability. Note that the analysis could not be conducted on Model 1 communities because there were too few replicates, and that the calculation of 1-month-old communities was identical for each of the null models. Data were fourth-root transformed before analysis. *P<0.05; ns = not significant.

Community age	Average dispersion among replicate actual communities	Count of the number of times average dispersion among replicate predicted communities exceeded the value observed among actual communities in 4999 model permutations.			
		Model 2	Model 3	Model 4	Model 5
1 month	0.04	349	338	321	354
		(P=0.070)	(P=0.068)	(P=0.064)	(P=0.071)
2 months	0.04	0	0	6	0
		(P<0.001*)	(P<0.001*)	(P=0.001*)	(P<0.001*)
3 months	0.04	0	0	678	6
		(P<0.001*)	(P<0.001*)	(P=0.136 ^{ns})	(P=0.001*)
4 months	0.04	0	0	71	23
		(P<0.001*)	(P<0.001*)	(P=0.014*)	(P=0.005*)
6 months	0.04	0	0	0	84
		(P<0.001*)	(P<0.001*)	(P<0.001*)	(P=0.017*)
7 months	0.08	0	0	708	14
		(P<0.001*)	(P<0.001*)	(P=0.142 ^{ns})	(P=0.003*)
9 months	0.07	0	0	1129	1085
		(P<0.001*)	(P<0.001*)	(P=0.226 ^{ns})	(P=0.217 ^{ns})
10 months	0.03	0	0	0	1618
		(P<0.001*)	(P<0.001*)	(P<0.001*)	(P=0.324 ^{ns})
11 months	0.07	0	0	4429	0
		(P<0.001*)	(P<0.001*)	(P=0.886 ^{ns})	(P<0.001*)
12 months	0.05	0	0	583	216
		(P<0.001*)	(P<0.001*)	(P=0.117 ^{ns})	(P=0.043*)

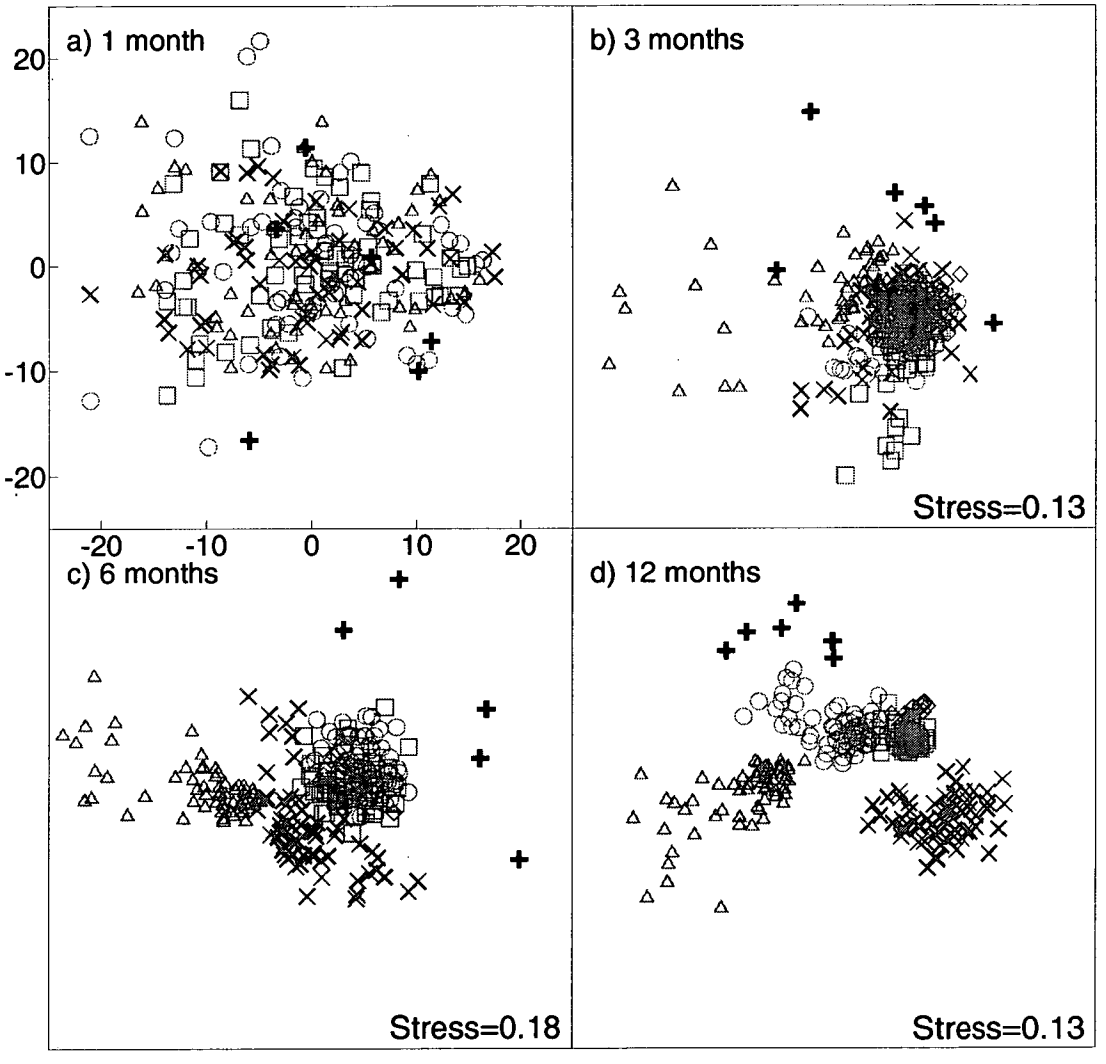

Figure 2 Ordination plots based on Bray-Curtis similarities (fourth root transformed data) among replicate actual communities (✚, n=6) and replicate Model 1 (◇, n=15), Model 2 (○, n=60), Model 3 (□, n=60), Model 4 (Δ, n=60) and Model 5 (×, n=60) communities, for several representative communities ages. PCO was used to represent distances among 1-month-old communities (because stress values in nMDS were so high), while nMDS plots were used to represent distances among communities aged 3-12 months. Note that the PCO plot would also have a high degree of stress and should be interpreted with caution, the cumulative variability explained by the first two axes was 28%.

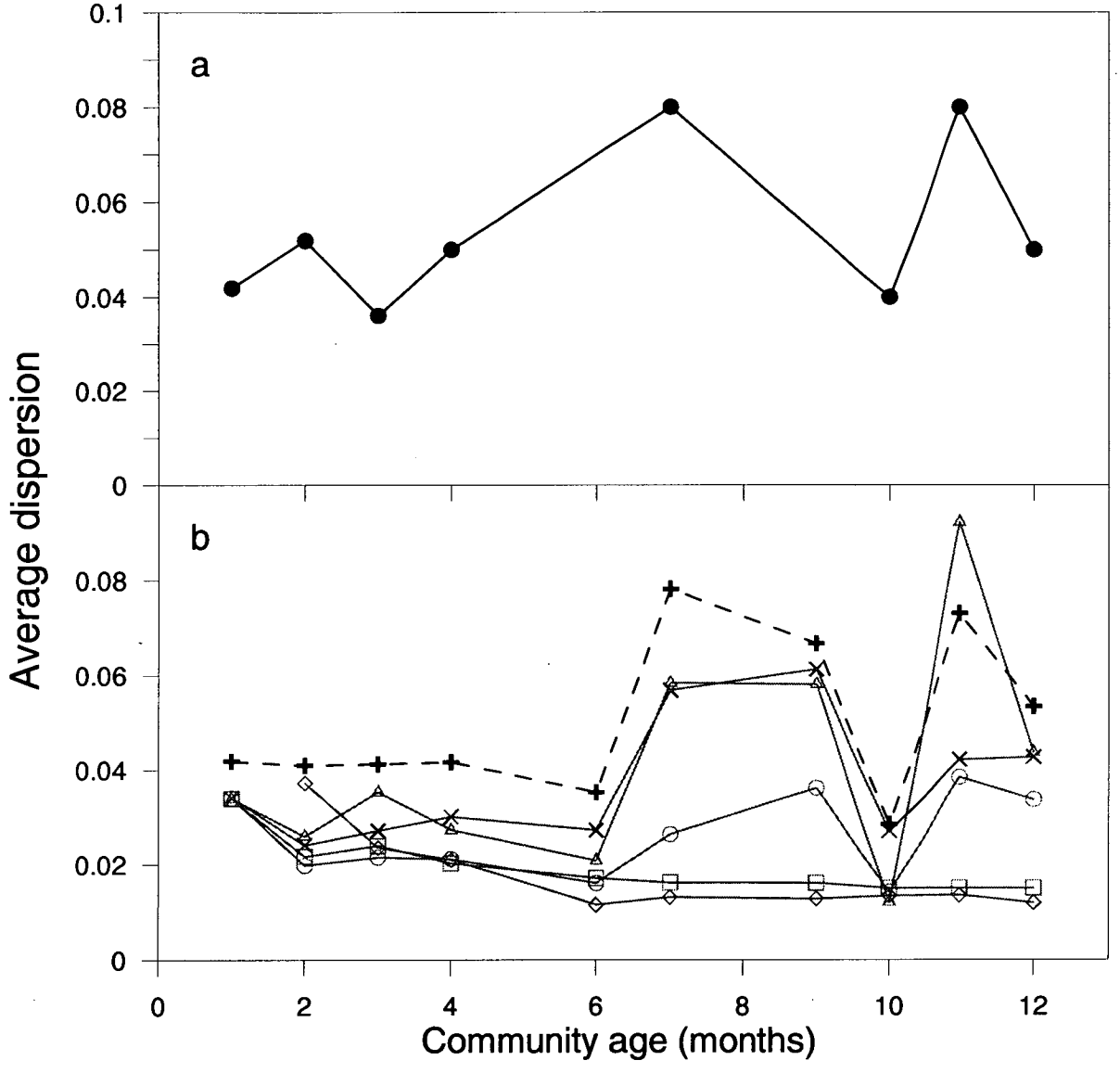

Figure 3 Change in average multivariate dispersion (Bray-Curtis) among a) replicate monthly recruitment data (●, n=6) and b) replicates of actual (✚, n=6), Model1 (◇, n=15), Model 2 (○, n=60), Model 3 (□, n=60), Model 4 (Δ, n=60) and Model 5 (×, n=60) communities, for each community age. Note that data presented for Models 2-5 are means of the average dispersion (see *Methods*).

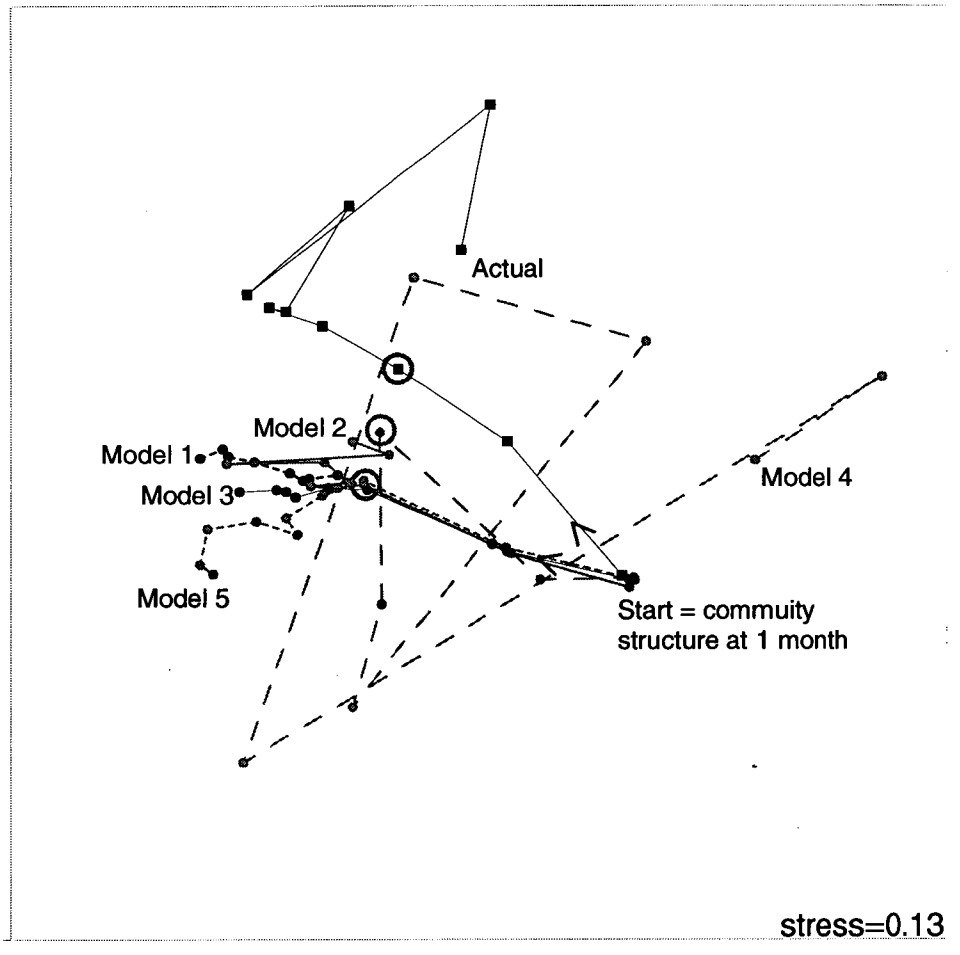

Figure 4 NMDS plot representing temporal trajectories (based on Bray-Curtis similarities of the fourth-root transformed data) for average communities obtained from actual (—▪—) and predicted communities; Model 1 (--•--), Model 2 (—•—), Model 3 (—•—), Model 4 (--•--) and Model 5 (--•--). Trajectories begin with 1-month-old communities, except for the Model 1 communities which begin with a 2-month-old community. Circles are used to indicate the position of each 3-month-old community; after this amount of development the structure of Model 1, 2, 3 and 5 communities diverged considerably as they developed.

4.4.3 Differences among model communities

Differences in the structure of the different model communities also varied depending on the age of the predicted communities (Table 4, Figures 2 and 4). For all models, the predicted communities at 1-month in age were similar (Table 4), simply because the technique used to generate communities of this age was the same for each model. As the predicted communities aged, the degree of difference grew larger, since *R* values tended to increase in magnitude with community age, as did the frequency of significant results (Table 4). This divergence is clearly seen in nMDS space, which shows that groups of replicate holdfasts from each model type became more distinct as communities age (Figure 2), and that the trajectories of the average community of each model diverge (Figure 4).

Comparisons defined *a priori* included: Model 1 vs. Model 2 communities (aim 1); Model 2 vs. Model 3 communities (aim 2); and, comparing Model 4 and Model 5 communities with each other and all other model communities (aim 3). Model 1 communities tended to be more similar in structure to Model 2 communities than any other predicted community type (Table 4, Figure 2). Model 2 and Model 3 communities were similar in early stages of development, but diverged significantly for communities greater than 4 months in age. Communities predicted by Model 4 were highly variable through time (Figure 4) and different to all other model communities in terms of richness (Figure 1b), evenness (Figure 1c) and multivariate community structure (Table 4, Figures 2 and 4). In contrast, dispersion amongst replicate communities generated by this model type was similar to that seen in Model 5 communities.

Table 4 Remaining pair-wise *a posteriori* ANOSIM analyses from Table 2. Tests compare communities generated by each model type for each community age. See Table 2 for details of the analysis. *P<0.05; ns = not significant.

R, *P*	Model 1	Model 2	Model 3	Model 4
1 month				
Model 1				
Model 2	n/a			
Model 3	n/a	-0.01, 4.21^{ns}		
Model 4	n/a	-0.01, 3.47^{ns}	-0.02, 0.98^{ns}	
Model 5	n/a	0.00, 3.05^{ns}	-0.02, 1.89^{ns}	-0.01, 2.74^{ns}
2 months				
Model 1				
Model 2	0.64, <0.001*			
Model 3	0.46, <0.001*	0.00, 0.42^{ns}		
Model 4	0.41, <0.001*	0.27, <0.001*	0.25, <0.001*	
Model 5	0.41, <0.001*	0.06, <0.001*	0.06, <0.001*	0.15, <0.001*
3 months				
Model 1				
Model 2	0.12, 0.20^{ns}			
Model 3	0.10, 0.21^{ns}	0.02, 0.14^{ns}		
Model 4	0.19, 0.12^{ns}	0.30, <0.001*	0.33, <0.001*	
Model 5	0.04, 0.29^{ns}	0.09, <0.001*	0.12, <0.001*	0.17, <0.001*
4 months				
Model 1				
Model 2	0.08, 0.17^{ns}			
Model 3	0.11, 0.14^{ns}	0.02, 0.05^{ns}		
Model 4	0.62, <0.001*	0.66, <0.001*	0.63, <0.001*	
Model 5	0.16, 0.11^{ns}	0.29, <0.001*	0.24, <0.001*	0.33, <0.001*
6 months				
Model 1				
Model 2	0.09, 0.20^{ns}			
Model 3	0.05, 0.25^{ns}	0.11, <0.001*		
Model 4	0.72, <0.001*	0.91, <0.001*	0.81, <0.001*	
Model 5	0.24, <0.001*	0.63, <0.001*	0.39, <0.001*	0.49, <0.001*
7 months				
Model 1				
Model 2	0.17, 0.03*			
Model 3	0.12, 0.07^{ns}	0.40, <0.001*		
Model 4	0.65, <0.001*	0.80, <0.001*	0.82, <0.001*	
Model 5	0.01, 0.43^{ns}	0.62, <0.001*	0.41, <0.001*	0.71, <0.001*

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9 months				
Model 1				
Model 2	0.05, 0.51^{ns}			
Model 3	0.21, 0.01*	0.30, <0.001*		
Model 4	0.58, <0.001*	0.58, <0.001*	0.77, <0.001*	
Model 5	-0.06, 0.74^{ns}	0.41, <0.001*	0.37, <0.001*	0.69, <0.001*
10 months				
Model 1				
Model 2	0.15, 0.04*			
Model 3	0.43, <0.001*	0.38, <0.001*		
Model 4	1.00, <0.001*	1.00, <0.001*	0.99, <0.001*	
Model 5	0.68, <0.001*	0.79, <0.001*	0.48, <0.001*	0.85, <0.001*
11 months				
Model 1				
Model 2	0.66, <0.001*			
Model 3	0.44, <0.001*	0.78, <0.001*		
Model 4	0.77, <0.001*	0.72, <0.001*	0.88, <0.001*	
Model 5	0.80, <0.001*	0.96, <0.001**	0.76, <0.001*	0.89, <0.001*
12 months				
Model 1				
Model 2	0.52, <0.001*			
Model 3	0.61, <0.001*	0.63, <0.001*		
Model 4	0.89, <0.001*	0.71, <0.001*	0.93, <0.001*	
Model 5	0.87, <0.001*	0.93, <0.001*	0.77, <0.001*	0.96, <0.001*

4.4.4 Testing for variability in recruitment.

The multivariate structure of recruits newly establishing in holdfasts varied among all months except between January and February, and April and July$_c$ (Table 5). While there was a significant overall difference in the degree of variability among replicates in these communities (Table 5), pair-wise *a posteriori* tests did not have sufficient power to detect differences in the structure of recruits between deployment dates (Table 5).

4.4.5 Analysis of interactions between individuals

Of those families that contributed most to the dissimilarities observed between actual communities and predicted communities, most showed a consistent type of interaction with the existing community (Table 6). There were examples of both positive (families Hiatellidae and Serpulidae) and negative (families Fissurellidae, Phyllodocidae, Arcturidae and Trochidae and Sub-order Caridea) interactions (Table 6). The families Sphaeromatidae and Terrebellidae, the Sub-order Gammaridea, the Class Ostracoda and an unidentified ophiuroid were less consistent in the nature of their interactions with the established community, usually because the models neither over- nor under-estimated the abundance of these taxa for several time intervals (Table 6).

There was little evidence to suggest that any one of the models was able to predict the abundance of an individual family with any more certainty than any of the others, at least for those families identified as having a high contribution to differences observed between predicted and actual communities (Table 6). Each model over- or under-estimated the total abundance of each of the taxa a similar number of times, except for the total abundance of the unidentified family of Ophiuroidea. The total abundance of this taxon was overestimated in most time intervals when using Models 1-3 and neither over or underestimated when communities were generated using Models 4-5.

Table 5 Results of pair-wise *a posteriori* tests between 1-month-old communities deployed on different dates, following analysis by PERMANOVA testing for variation in community structure ($F_{7,40}$=6.19, P=0.0002, 4999 permutations) and PERMDISP testing for variation in community variability ($F_{7,40}$=3.04, P=0.007, 4999 permutations). Comparisons using PERMDISP are only presented if a significant difference was identified using PERMANOVA. Monte Carlo P-values were used in the PERMANOVA analysis because the number of unique values of the test statistic (t) was relatively low. Significance was adjusted by the sequential Bonferroni procedure to control the Type 1 error rate. * = significant; ns = not significant.

Paired comparison	PERMANOVA			PERMDISP		
	t	# unique values of t	Adjusted Monte Carlo P-value	t	# Permutations	Adjusted P-value
(Jan 98, Feb 98)	1.33	462	0.11^{ns}	0.31	462	n/a
(Jan 98, Mar 98)	2.17	461	0.03*	0.71	462	6.79^{ns}
(Jan 98, Apr 98)	2.40	461	0.02*	0.10	462	2.78^{ns}
(Jan 98, Jul 98)	2.11	462	0.02*	4.90	462	0.16^{ns}
(Jan 98, Oct 98)	2.87	462	0.02*	0.32	462	5.32^{ns}
(Jan 98, Nov 98)	2.37	462	0.01*	2.26	462	0.45^{ns}
(Jan 98, Dec 98)	2.00	462	0.03*	0.49	462	6.93^{ns}
(Feb 98, Mar 98)	1.99	462	0.03*	0.06	462	0.96^{ns}
(Feb 98, Apr 98)	2.18	462	0.02*	0.33	462	7.00^{ns}
(Feb 98, Jul 98)	2.15	459	0.02*	2.60	462	0.22^{ns}
(Feb 98, Oct 98)	3.26	461	0.01*	0.10	462	1.88^{ns}
(Feb 98, Nov 98)	2.47	462	0.02*	1.75	462	1.49^{ns}
(Feb 98, Dec 98)	2.48	462	0.02*	0.55	462	6.72^{ns}
(Mar 98, Apr 98)	2.03	461	0.03*	0.55	462	7.36^{ns}
(Mar 98, Jul 98)	2.37	461	0.02*	5.46	462	0.08^{ns}
(Mar 98, Oct 98)	4.08	462	0.01*	0.28	462	4.73^{ns}

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(Mar 98, Nov 98)	2.91	461	0.01*	2.71	462	0.28 ^{ns}
(Mar 98, Dec 98)	3.01	462	0.01*	1.19	462	4.20 ^{ns}
(Apr 98, Jul 98)	1.51	462	0.08 ^{ns}	2.76	462	n/a
(Apr 98, Oct 98)	4.03	462	0.01*	0.31	462	6.02 ^{ns}
(Apr 98, Nov 98)	2.54	461	0.02*	1.65	462	2.42 ^{ns}
(Apr 98, Dec 98)	2.97	462	0.01*	0.20	462	3.56 ^{ns}
(Jul 98, Oct 98)	2.80	461	0.01*	4.21	462	0.06 ^{ns}
(Jul 98, Nov 98)	1.80	462	0.04*	0.73	462	6.60 ^{ns}
(Jul 98, Dec 98)	2.32	462	0.03*	4.47	462	0.12 ^{ns}
(Oct 98, Nov 98)	2.39	462	0.03*	2.28	462	0.49 ^{ns}
(Oct 98, Dec 98)	2.55	462	0.02*	0.72	462	7.20 ^{ns}
(Nov 98, Dec 98)	1.88	461	0.04*	1.96	462	0.92 ^{ns}

Table 6 Summary of results from a series of SIMPER analyses, used to identify which taxa contributed most to differences observed between actual communities and predicted communities. A total of 45 comparisons (9 time intervals between 2 and 12 months of age by 5 models) were made. Note that each SIMPER analysis was arbitrarily stopped once 40% of the variance among samples was accounted for and that results are presented for only a subset of the taxa identified.

Taxon		Percentage of times taxa was identified (out of 45)	Number of times abundance was overestimated (underestimated) across 9 time intervals.				
			Model 1	Model 2	Model 3	Model 4	Model 5
Family Hiatellidae	bivalve	84.4%	0(6)	0(8)	0(6)	0(9)	0(9)
Family Fissurellidae	keyhole limpet	80.0%	9(0)	7(0)	8(0)	3(0)	9(0)
Family Phyllodocidae	errant polychaete	80.0%	8(0)	7(0)	8(0)	5(0)	8(0)
Family Serpulidae	sedentary polychaete	75.6%	0(6)	0(7)	0(5)	1(8)	0(7)
Family Arcturidae	isopod	75.6%	8(0)	8(0)	8(0)	2(0)	8(0)
Sub-order Caridea	decapod	64.4%	7(0)	7(0)	9(0)	1(0)	5(0)
Family Trochidae	gastropod	62.2%	6(0)	5(0)	7(0)	3(0)	7(0)
Class Ostracoda	ostracod	53.3%	4(2)	5(1)	4(1)	2(3)	1(1)
Sub-order Gammaridea	amphipod	51.1%	5(0)	4(0)	5(0)	4(1)	4(0)
Family Sphaeromatidae	isopod	48.9%	4(0)	5(0)	5(0)	2(0)	6(0)
Unidenified Ophiuroidea	brittle star	44.4%	8(0)	6(0)	6(0)	0(0)	0(0)
Family Terebellidae	sedentary polychaete	44.4%	4(0)	3(2)	4(1)	1(2)	2(1)

4.5 Discussion

We broadly classified the processes that may be important in determining macrofauna community structure into recruitment, adult-adult interactions (which by necessity included natural mortality) and recruit-adult interactions (which included pre- and immediately post-settlement interactions). Our aim was to describe the change in the relative contribution of each of these broad types of

process to community structure during assembly of a community dominated by mobile organisms. Assembly over the course of 12 months was examined because the effects of an increased rate of recruitment can be simulated by increasing the age of the community in the absence of disturbance (Chapter 3) and because processes influencing successful recruitment and thus community structure in younger communities, may not necessarily manifest as differences in community structure in older communities (Holloway and Keough 2002).

4.5.1 The importance of recruitment

Variability in monthly recruitment explained a large proportion of the community structure in actual communities. However, communities predicted using recruitment data alone were significantly different from actual communities (see also Chapter 3). Additionally, the influence of recruitment decreased as the communities aged. These results can be interpreted in terms of the recruit-adult hypothesis (Gaines and Roughgarden 1985, Roughgarden et al. 1988, Connolly and Roughgarden 1999a, Connolly et al. 2001; see Chapter 3 for a more detailed analysis), which predicts that the structure of a more crowded community is more likely to reflect post-settlement interactions than recruitment (Dayton 1971).

In younger communities, there was little indication to suggest that a carrying capacity existed that could potentially limit the influence of recruitment. However, older Model 1 and 2 communities were significantly different from one another, and the Model 2 communities were more similar to actual communities than the Model 1 communities. This provides evidence to suggest that a carrying capacity on total abundance existed in these communities,

although the actual limit to total abundance was unclear because there were a few actual communities with unusually high total abundances (see also Chapter 2). While the addition of a carrying capacity improved the fit between model and actual communities, it was not sufficient to completely explain community structure in actual communities; Model 2 communities, although more similar to actual communities than Model 1 communities, were still significantly different from actual communities. This means that the interactions that occur among species, emigration, and/or the natural mortality of individuals, must also play an important role in these communities.

Given these results, an obvious question is whether total abundance is limited without any change to the relative abundances of families within a holdfast community or, alternatively, whether limits to abundances lead to intense competition that alters the relative abundances of the different families. Similar mobile marine communities have been described as potentially limited by the availability of resources (*e.g.* food, Edgar 1993; and space, Smith and Rule 2002) which could lead to competition. Competition may occur between potential recruits and established individuals or among members of the established community; Models 3-5 were developed to try to separate the influence of these two types of interaction on community structure.

4.5.2 Interactions between potential recruits and established individuals (recruit-adult interactions)

Interactions between potential recruits and established individuals that could have influenced our results can take the form of pre-settlement interactions or

immediate, post-settlement interactions (before census for recruitment). This covers a broad range of different types of interaction. Potential settlers may be attracted or inhibited by chemicals which may be water-borne or associated with the substratum or established community (Pawlik 1992). Alternatively, they may be influenced by water movements around the substratum, which may be linked to the physical structure of the established community (Smith et al. 1996, Bertness and Leonard 1997) or to biologically generated water movements (*e.g.* suspension feeders; Butman 1987). If an individual does manage to settle, it may be killed or forced to migrate through physical disturbance (irritation; *e.g.* Dahms et al. 2004, Dahms and Qian 2005) or predation (*e.g.* Osman and Whitlach 1995a, b) by other organisms. Note that factors linked with the physical structure of the holdfasts have been ignored since the overall size and shape of each holdfast in this study was identical.

The most likely result of these kinds of interactions would be a divergence in the assembly trajectories observed for Model 2 and Model 3 communities. Model 3 communities which allowed early settlers to hold positions within the community over later settlers should be more like actual communities than Model 2 communities. As predicted, young Model 2 and 3 communities were not significantly different, but increasingly diverged as the communities aged. Recruitment was variable over this time period and thus cannot explain the similarities observed in younger communities. However, contrary to our prediction, as the model communities aged, Model 2 communities became slightly more similar to actual communities than Model 3 communities (although both were still significantly different from actual communities). The most likely cause of differences between actual and Model 3 communities is that Model 3

allowed only complete dominance of the holdfast by early recruits, whereas in actual communities, the recent recruitment history is likely to have some influence over community structure. A proportion of the available potential recruits should be able to invade successfully despite the defense of the community by early recruits (*e.g.* through facilitation) and adult-adult interactions may allow new recruits access. Smith (2000), also observed that recent sporadic recruitment of rare species appeared to influence macrofauna community structure in *Ecklonia radiata* holdfast communities, because communities collected at multiple sites within two locations in New South Wales grouped (in nMDS space) by time of collection rather than by site.

4.5.3 Interactions among residents (adult-adult interactions)

Adult-adult interactions were assumed to have a negative effect on the abundance of each family. Positive adult-adult interactions may play an important role in many communities (Bruno et al. 2003) but would not influence the abundance of resident taxa in this study, unless through enhanced reproduction. Reproductive effects in our study were more likely to be observed in brooding species, since offspring are more likely to remain within the holdfast. Brooding species, *e.g.* polychaetes (Levin 1984) and Crustacea (Thiel and Vásquez 2000) have been identified as ecologically important in similar communities. However, we identified only two families that were consistently underestimated in our models, namely the bivalve family Hiatellidae which was represented by a single species, *Hiatella australis*, and the polychaete family Serpulidae, which was predominantly made up of *Galeolaria caespitosa*. Neither of these species are known to be brooders.

Negative, adult-adult interactions could have included predation and/or competition leading to emigration (*e.g.* Moksnes 2004, Junkins et al. 2006) or mortality. Interference competition among more sessile organisms (*e.g.* tube dwelling polychaetes; Levin 1982) may not necessarily result in mortality or emigration and was under-represented in our models. By necessity our measure of the impacts of these adult-adult interactions also included the impacts of natural mortality and emigration due to changes in habitat requirements (*e.g.* if the holdfast is only used as a nursery habitat), or of transitory species that are likely to move in and out of these habitats regularly (Costello and Myers 1996, Norderhaug et al. 2002, Jorgenson and Christie 2003). The impacts of these latter processes are probably less important in determining net mortality and emigration than adult-adult interactions, because species that would only use a holdfast during an early stage of development were rare (a single individual rock lobster, 1 species of sea urchin and 2 species of fish), and because the immigration of transitory species should balance emigration. The influence of natural mortality in this type of community is unknown and in general is very difficult to assess experimentally (*e.g.* copepods, Hirst and Kiørboe 2002).

Models 4 and 5 incorporated negative adult-adult interactions in community assembly. Theoretically, communities predicted using these models should be more like actual communities than Models 1-3 because they allow for the removal of residents and provided an opportunity for new recruits to establish. The difference between the two models was that mortality was random in Model 4 communities and family-specific in Model 5 communities. The community structure and dynamics of Model 4 communities were, not surprisingly, unrealistic and will not be considered further; mortality and emigration are

unlikely to be random across taxa, given the diversity of organisms and life-history strategies found in members of this type of community (*e.g.* Moore 1972, Ojeda and Santelices 1984, Smith et al. 1996).

The comparison of Model 2 and 3 communities indicated that new recruits continued to enter older more established communities, despite an apparent carrying capacity on abundance. Given this result, Model 5 communities were expected to be most like actual communities because they provided opportunity for new recruits to enter the community. While Model 5 communities clearly correlated with observed levels of variability seen in actual communities, they were not more similar in community structure to actual communities than other predicted communities (in the time-scale examined here). Thus, adult-adult interactions appear to have less influence in determining community structure and development than do recruitment and recruit-adult interactions.

4.5.4 Community variability

Results on the variability seen in natural communities and model communities were interesting and warrant further discussion. Communities constructed by the simple accumulation of recruits over time (Model 1) became less variable (among replicates) as they aged (see also Chapter 3), presumably because the significant fluctuations in monthly recruitment that we observed were averaged out (Underwood and Chapman 2006). A similar pattern was observed in Model 3 communities because early colonists (which colonised during times of low variability in the recruitment signal) were able to obtain space in the community and prevent the influence of later fluctuations in recruitment. This pattern was

not observed in Model 2 communities because early and late colonists had the same probability of being selected.

Variability among replicate actual communities reflected the ongoing influence of recruitment throughout the life of the community. While this pattern was similar to that observed for Model 2 communities, the mechanism generating these patterns was probably different; variability observed in actual communities was probably more influenced by variability in recruitment than in Model 1 and 3 communities, not because early and late colonists had the same probability of recruiting (as in Model 2), but because mortality and emigration provided space in the community for new recruits to establish. Models 4 and 5 did incorporate mortality and emigration, and space pre-emption and the variability seen among replicate communities generated by these models was most like that observed in actual communities. Thus, while the impact of adult-adult interactions on community structure was minimal, this type of interaction did appear to influence variability in community structure. The mechanism for this appears to be indirect, in that by incorporating mortality and emigration, the community became more susceptible to the influence of variability in recruitment. This indirect effect of recruitment on community variability provides a mechanism for recruitment to influence community variability at small spatial scales. High levels of small-scale variability is a commonly observed phenomenon in marine benthic systems (*e.g.* Lively et al. 1993, Underwood 1996, Underwood and Chapman 1996, Dunstan and Johnson 1998, Benedetti-Cecchi 2001, Anderson et al. 2005a, Fraschetti et al. 2005), but recruitment is usually only described as a potential mechanism when there are small-scale differences in topography (*e.g.* Underwood and Chapman 1996, Coleman et al. 2002).

The ongoing influence of recruitment mediated by species interactions fits well with current theories on invasion resistance in communities. Traditionally, species richness has been thought to be important in determining the abilities of a community to resist invasion (Elton 1958). More recently, connectivity and interaction topologies among resident species have been shown to have a greater influence on the likelihood of successful invasion (Davis et al. 2000, Dunstan and Johnson *in press*).

4.5.5 Interactions among individuals

Families that had a high contribution to the differences observed in the structure of model and actual communities were identified. The nature of the interaction between recruits of these families and the established community was not consistent among the different families. However, for any particular family, the nature of the interaction was usually consistent, regardless of the model employed or the age of the community. For most families, familial abundances were overestimated in model communities (*e.g.* families Fissurellidae, Phyllodocidae, Arcturidae and Trochidae and Sub-order Caridea). In contrast, the families Hiatellidae and Serpulidae were consistently under-estimated in model communities.

Species interaction topologies may be highly complex and not fully resolvable in species-rich communities (Johnson and Seinen 2002). Such complex interactions make it very difficult to identify the mechanisms driving community dynamics, through experimentation (Underwood et al. 1983). Our results were reassuring, because there was some evidence to suggest that there was consistency in the net

effect of the established community on the recruitment of particular families. Thus it may be possible to identify consistent species-level interactions that influence community structure and to gain a more thorough understanding of the mechanisms driving community pattern in these communities.

4.5.6 Conclusions

The results of this experiment were sometimes contradictory. Results contrasting the structure of Model 2 and 3 communities suggested that recruits continued to find space in communities that were likely to have reached a carrying capacity, and yet removing individuals to provide access for these recruits did not improve the fit of predicted communities to actual communities (although these models did generate similar levels of variability among replicates). This most likely reflects that the established community differentially allows new recruits to enter the community, but the identity of these recruits is influenced by established individuals through both positive and negative interactions.

Positive interactions between potential recruits and the established community were identified as important for at least two families. Both of these taxa were highly abundant and could significantly impact on the observed community structure, although this was limited in the multivariate analysis through a fourth-root transformation. Some of our models did partially account for negative recruit-adult interactions by allowing early recruits to obtain positions within the community over later recruits. However, in this type of interaction the composition of the recruiting assemblage still reflected the community composition that developed in uninhabited holdfasts. Negative interactions may also act to change the relative abundances of the different recruiting families.

These results have implications for the way we estimate recruitment in models of marine community dynamics. It seems very likely that predicted and actual communities were different largely because recruitment to bare space is a poor indicator of the actual recruitment of organisms to an established community.

5 ROBUSTNESS OF SURROGATES OF BIODIVERSITY IN MARINE BENTHIC COMMUNITIES

5.1 Abstract

The usefulness of surrogates to estimate complex variables describing community structure, such as the various components of biodiversity, is long established. Most attention has been given to surrogates of species richness and species diversity, and has focused on identifying a subset of taxa as a surrogate of total community richness or diversity. In adopting a surrogate measure, it is assumed that the relationship between the surrogate(s) and total richness or diversity is consistent in both space and time. These assumptions are rarely examined explicitly. We examined the robustness of potential surrogates of familial richness and multivariate community structure for macrofauna communities inhabiting artificial kelp holdfasts by comparing among communities of dissimilar ages and among communities established at different times of the year. This is important because most benthic 'landscapes' will be a mosaic of patches reflecting different intensities, frequencies and timing of disturbances. The total abundance of organisms and familial richness of crustaceans or polychaetes were all good predictors of total familial richness (R^2 > 0.68). In contrast, while the familial richness of other groups such as molluscs and echinoderms were well correlated with total familial richness for communities at an early stage of development, the strength of these relationships declined with community age. For multivariate community structure, carefully selected subsets of ~10% of the total taxa yielded similar patterns to the total suite of taxa irrespective of the age of the community. Thus, useful surrogates of both familial richness and multivariate community structure can be identified for this type of community. However, the choice of technique for selecting surrogate taxa depends largely on the nature of the pilot data available, and

careful selection is required to ensure that surrogates perform consistently across different aged communities. While the specific taxa selected as surrogates will vary among different communities and possibly even among similar communities at different sites, the techniques and the concepts we address are applicable to any community type.

5.2 Introduction

Biodiversity is an important and fundamental concept in ecology, but it is also highly complex because it encompasses functional system components in addition to structural components such as genetic, species, habitat and ecosystem diversity (Franklin 1988, Noss 1990, Vane-Wright et al. 1991). Accordingly, the assessment of biodiversity usually relies on a proxy such as species richness or diversity. However, even attempting to enumerate all species is a time-consuming, labour-intensive and skilled task for conservation biologists (Daily and Ehrlich 1995, Kitching et al. 2001), so that extrapolative and other techniques will always be sought to optimise efficiencies. This is particularly true while taxonomy continues to be a low priority for both researchers and funding bodies (Valdecasas and Camacho 2003, Wheeler et al. 2004), and is conducted in relative isolation from the other disciplines in the life sciences (Dayrat 2005).

Research has long established the potential usefulness of one type of extrapolative approach, namely the use of various indices to estimate and monitor ecological impact and describe ecosystem integrity (Noss 1990). These indices are known as biological indicators or bioindicators and their application has been widespread across terrestrial (*e.g.* Kremen 1992, Samways and Steytler

1996, Warman et al. 2004), freshwater (*e.g.* Karr 1981, Savage 1982, Fore et al. 1996) and marine environments (*e.g.* Olsgard et al. 2003).

Of several different kinds of indices, each with their relative merits (see Noss 1990, McGeoch 1998), surrogates for biodiversity are among the most commonly used (McGeoch 1998). This approach usually involves selecting a subset of species (or higher taxon) from a community as a surrogate of either the biodiversity of another taxon or as a surrogate of the total biodiversity of a community. In these studies, the aim is usually to monitor or compare ecosystem properties (such as biodiversity) or to detect environmental impact (*e.g.* Karr et al. 1987, Gaston and Williams 1993, Gaston and Blackburn 1995, Gaston 1996b). Taxa may be selected because they are abundant or are known to be sensitive to particular environmental perturbations, or because of a predilection towards particular taxa, which may simply reflect available taxonomic expertise.

In the case of monitoring taxa thought to be sensitive to environmental impact, considerable effort, particularly in freshwater systems, has been given to ratifying indicators of impact and testing underlying assumptions, (*e.g.* Karr et al. 1987, Barbour et al. 1992, Diamond et al. 1996, Fore et al. 1996). However, this is not the case in the use of surrogates for more general monitoring of biodiversity where, in only a few cases, attention has been given to comparing the performance of a range of potential choices of surrogates (*e.g.* Oliver and Beattie 1996, Lund and Rahbek 2002, Anderson et al. 2005b) or to the underlying assumptions (McGeoch 1998). The key assumption made in attempting to identify and apply surrogates of total biodiversity is that the

relationship between the selected surrogate taxa and total biodiversity is constant in space and time (Colwell and Coddington 1994). Spatial consistency in the identity of surrogates has been examined and, at least in some cases, it is clear that surrogates should not be applied across regional spatial scales because species relationships are not necessarily the same in different regions (Beccaloni and Gaston 1995, Gaston 1996b, a, Anderson et al. 2005b). Surprisingly however, the assumption that, within any particular location, the relationship between the surrogate and total biodiversity is constant through time (*e.g.* Kitching et al. 2000) has received scant attention. Lack of discussion of this important aspect of the application of surrogacy arguably reflects that the majority of work employing surrogates has focused on comparing biodiversity among sites rather than through time, even though samples are usually pooled across several sampling periods (*e.g.* Pearson and Cassola 1992, Beccaloni and Gaston 1995, Gaston and Blackburn 1995, Erdmann and Caldwell 1997, Garson et al. 2002, Lund and Rahbek 2002, Olsgard et al. 2003, Warman et al. 2004). It is usually assumed (often implicitly) that differences in biodiversity indicated from samples collected at different sites and at different times is due to spatial variability. It is therefore assumed that surrogates are temporally consistent.

It is well recognised that community structure may vary temporally depending on successional status (*i.e.* disturbance history) (*e.g.* Dean and Connell 1987a) and seasonal effects. Moreover, these two factors may interact, such that the relative abundance of a taxon for a given successional state may depend on the timing of the original disturbance (Dayton et al. 1984, Chapman and Johnson 1990, Underwood and Anderson 1994, Nandakumar 1996). While changes in the relative abundance of a suite of taxa does not necessarily infer poor

suitability as a surrogate of total biodiversity, it is nonetheless important to establish robustness in the performance of putative surrogates in the face of temporal change in community structure. Thus, suitable surrogates for monitoring biodiversity are those that correlate with changes in biodiversity whether due to spatial variability, succession, season or disturbance (Colwell and Coddington 1994). Note that in this context, the assessment of the performance of surrogates in monitoring biodiversity differs from the traditional approach used to assess surrogates of environmental impact. Good surrogates of environmental impact are relatively static through space and time across reference sites but sensitive to impact levels (Karr et al. 1987, Underwood and Peterson 1988, Barbour et al. 1992, Glasby and Underwood 1998). Thus, surrogates intended to detect specific environmental impacts (often based on sensitive or intolerant taxa or functional groups; *e.g.* Barbour et al. 1992) will not necessarily be useful as surrogates to monitor or compare total biodiversity within or between sites. Moreover, surrogates of total diversity are more likely to be based on the species or familial richness of a single higher level taxon or the abundance of several taxa (Hammond 1994).

In this chapter we explore whether temporal variability is an important consideration in the selection of a structural biodiversity surrogate by examining the effects on surrogate performance of community age and the season of sampling, two distinct components of temporal variability in community structure. By doing so we also explore several potentially useful techniques to define surrogates and compare their performance. We use subtidal marine communities inhabiting artificial kelp holdfasts as a model system and, given that biodiversity can be defined validly in a number of ways (Noss 1990), we

examine both univariate and multivariate indices of familial biodiversity. We show that temporally stable surrogates can be identified for communities of different ages, and across different seasons of initial deployment and final assessment. However, exactly which taxa to use depends on the particular community in question. Moreover, the choice of which technique to use for selecting surrogate taxa depends largely on the nature of the reference data available.

5.3 Methods

5.3.1 Experimental design and field work

Artificial kelp holdfasts (hereafter 'holdfasts') were of similar size and physical complexity to the holdfasts of *Ecklonia radiata*, the most common species of kelp in southern Australia. Holdfasts were deployed to concrete supports set out on a grid over sand adjacent to a healthy *E. radiata* dominated reef in the Derwent River Estuary, Tasmania, Australia (42° 57.7' S, 147° 20.5 E). Holdfasts were deployed each month for 13 months beginning in December 1997. At each deployment, sufficient holdfasts were established to collect 6 replicates each subsequent month until January 1999. Due to poor weather, holdfasts were neither collected nor deployed in September, while collections were not possible in June. For treatments deployed in December 1997, 4 replicates (rather than 6) were collected each subsequent month. Thus, a total of 408 holdfasts were deployed to and recovered from random positions on the grid. Further details on the experimental design and construction of holdfasts are described in Chapter 1.

Solitary animals retained on a 1mm sieve were identified where possible to the level of family, the most notable exception being amphipods, which were identified to sub-order. Colonial organisms were not enumerated because they were very rare. We deemed taxonomic resolution to the level of family as the optimal cost-benefit trade-off given the large abundance of organisms encountered (148,841 individuals), and that family-level patterns typically reflect patterns at the species-level (Williams and Gaston 1994, Faith et al. 1995, James et al. 1995, Somerfield and Clarke 1995, Balmford et al. 1996, Olsgard et al. 1997, Mistri and Rossi 2001, Dahl and Dahl 2002, Olsgard et al. 2003, Anderson et al. 2005a, Anderson et al. 2005b).

5.3.2 Surrogacy analysis – Univariate surrogates of community richness

Higher level taxa likely to prove suitable surrogates are those that are proportionally abundant and rich. In our communities, the Crustacea, Mollusca, Polychaeta and Echinodermata were all potential candidates. Polychaetes (Olsgard and Somerfield 2000, Olsgard et al. 2003) and molluscs (Gladstone 2002) in particular have been suggested as possible surrogates of marine macrofauna communities in soft sediment and on rocky shores respectively because they are both abundant and ecologically important groups. The total abundance of all fauna counted within a holdfast was also used because it is the easiest of all community properties to enumerate. Thus, any surrogate taxon selected must be able to out-perform total abundance as a surrogate to be cost-effective.

The average familial richness (by deployment date and community age) of each taxonomic group and the average total abundance of all organisms was recorded and plotted against the average total familial richness (averages were of each group of 6 replicate holdfasts). Regression analysis was used to compare the goodness of fit (R^2) for each potential surrogate. Good surrogate taxa will have a high R^2 value reflecting a less noisy and thus more predictable relationship with richness. While we acknowledge that the familial richness of each taxonomic group is not independent of total familial richness and that this may be problematic in regression analysis (Schulze et al. 2004), we proceeded with the analysis in this way simply because the focus of the work was to evaluate how well the richness of a specific taxon was correlated with total richness.

If surrogate taxa are robust, then the relationship between each potential surrogate and total richness should not change with community age or deployment date. This premise was examined using analysis-of-covariance. Because of evidence of a correlation between community age and richness (at least for colder months), regression analysis was also used to determine whether the goodness-of-fit (*adjusted* R^2) of the relationship between richness of particular taxa and total richness varied with community age. *Adjusted* R^2 was used because the degrees-of-freedom varied for the various community age categories.

5.3.3 Surrogacy analysis – Multivariate surrogates of community pattern

We compared several approaches to select subsets of families that may reflect the multivariate patterns seen in the complete kelp holdfast communities in the experiment. The first was a taxonomic approach where all families within a higher taxon (usually phylum) were selected. We also used two techniques within the PRIMER5 statistical software package to select subsets of families, namely BVSTEP (Clarke and Warwick 1998, 2001) and SIMPER (Clarke and Warwick 2001). Surrogates selected using these techniques were compared with surrogates defined by random selections of taxa and selections of the numerically abundant taxa. The performance of each subset of surrogates was tested by comparing the matrices of similarities between all community ages and deployment dates for each surrogate set with the equivalent similarity matrix determined from the complete faunal complement.

5.3.3.1 Taxonomic approach

The four higher taxa selected were the same groups used to assess 'univariate surrogates' (Mollusca, Crustacea, Polychaeta and Echinodermata). All families within each of these groups were identified and each higher group was considered separately in contrasting the 'treatments' of community age and deployment date. Thus, a similarity matrix describing the similarity between each pair of 'treatments' was produced for each of the higher taxa.

5.3.3.2 SIMPER

SIMPER is used to identify those taxa that either contribute most to the average similarity within a treatment (*i.e.* between replicates) or to the average dissimilarity between two treatments (Clarke and Warwick 2001). We used SIMPER to identify families that contributed most to the average similarity among replicate communities of a particular deployment date. Since a suitable surrogate family must also occur consistently within holdfasts, the ratio of the average similarity to its standard deviation (SIM/SD) for each family (see Clarke and Warwick 2001) was also used to select families. Data were first transformed using a fourth-root transformation. For each deployment date selected as a reference point (arbitrarily January-April 1998), results of within-group average similarities were presented for each community age. Families were included in the surrogate set for a particular deployment date if they were selected for at least one community age. The number of families included within a surrogate set generated by SIMPER was therefore variable depending on deployment dates.

Because SIMPER was used to look for similarities within treatments rather than among treatments (as it is only able to make pair-wise comparisons between treatments), we also tested whether the results from the SIMPER analyses were consistent regardless of which deployment date or community age was selected. This was done by identifying the surrogate set for each treatment combination of deployment date and community age and comparing these surrogate sets using the Bray-Curtis similarity measure (Bray and Curtis 1957). Surrogate sets were compared across community ages for a given deployment date, and across

deployment dates for a given community age. Each surrogate set was compared to a reference point (either the first deployment date or first community age) to look for directional deviation from that point. A directional decline in Bray-Curtis similarity would suggest that the surrogate set identified by SIMPER indicated a gradual and directional change in community composition. Looking for a directional change is important because the Bray-Curtis measure is of overall similarity, not absolute community structure (*i.e.* the community structure of two samples of identical Bray-Curtis similarity to a given reference community may be dissimilar). Uniformly low Bray-Curtis values would suggest that there was no consistency in families selected by SIMPER across deployment dates or community ages. Note that we also conducted these analyses using a different arbitrary reference point (viz. the average surrogate subset), but since the interpretation of the results was similar this analysis is not presented.

5.3.3.3 BVSTEP

BVSTEP is a stepwise algorithm used most frequently to identify environmental variables that best correlate with patterns in biological data (Clarke and Warwick 2001). The routine identifies combinations of environmental variables that yield the highest rank correlation between similarity matrices based on biological and environmental variables (where similarity matrices describe similarities among samples). In a similar approach, if the original data matrix of biological variables is used instead of the environmental variables, BVSTEP can be used to exclude taxa that are redundant in explaining community level pattern (Clarke and Warwick 1998).

We used BVSTEP to identify potential surrogate sets of families (regardless of which higher taxon they came from), which best reflected community level patterns through time for each of four deployment dates (January-April 1998). Early deployment dates were selected because this yielded longer time series in community development. December 1997 was not used because there were fewer replicates for this month. Similarity matrices describing Bray-Curtis similarity among communities of different ages but identical deployment date were based on fourth-root transformed data. Selections of taxa in defining surrogate sets were based on highest values of the weighted or harmonic Spearman rank correlation coefficient, ρ_w (Clarke and Ainsworth 1993). We selected the best results presented by BVSTEP for combinations of 5, 10, 12, 15 and 20 families. Thus, we obtained surrogate sets generated by BVSTEP for four different deployment dates, and for each of these deployment dates we had surrogate sets of 5, 10, 12, 15 and 20 families. Note that the total number of families detected across all holdfasts combined was exactly 100.

5.3.3.4 Comparing multivariate surrogate sets

We then examined whether the 'optimal' surrogate sets identified by a taxonomic approach, SIMPER and BVSTEP performed any better than combinations of 5, 10, 12, 15 and 20 families selected either randomly or on the basis of greatest total abundance. If the putative 'optimal' surrogate sets are to be useful, they must perform better (achieve a higher ρ_w) than selection by random choice or on the basis of abundance, which are both quicker and easier ways of selecting surrogate taxa.

Performance was assessed by how well each multivariate surrogate set predicted the multivariate relationships across all treatments of deployment date and community age based on the complete suite of families. This was accomplished using 'a second stage analysis' (Somerfield and Clarke 1995) in which similarity matrices (describing similarities between treatments of deployment date and community age) based on surrogate sets were correlated with the equivalent similarity matrix based on all families (Anderson et al. 2005b). Correlations were calculated for each comparison using the weighted Spearman rank correlation coefficient (note that qualitative patterns in correlations were similar to those using the Spearman or Kendall correlation coefficients). Results of the second stage analysis can be presented using a non-metric multidimensional scaling (nMDS) plot to display patterns in the degree of correlation (Somerfield and Clarke 1995, Anderson et al. 2005a, b). However since an nMDS plot is only a 2-dimensional estimation of *all* relationships (including those between surrogates), we present correlations between each surrogate set and the complete suite of families in table form.

Similarity matrices based on surrogate families that are highly correlated with the similarity matrix using all families should produce similar patterns in nMDS plots. Accordingly, nMDS plots were generated for some results to demonstrate how patterns changed as correlations between similarity matrices based on the full data set and those based on subsets of species, declined. Data from March 1998 (which gave the best and worst correlations depending on the number of families selected), were used in this analysis. Note that some treatments were deleted from displayed plots to clarify presentation, but they were not deleted from the actual analysis.

5.4 Results

5.4.1 Univariate surrogates of community richness – surrogates by taxonomic group

The relationship between each taxonomic group's average familial richness and average total familial richness was linear, while the relationship between average total abundance of all individuals and average familial richness was a power curve (Figure 1). Surprisingly, the best surrogate of average total familial richness (highest R^2) was the average total abundance of all individuals (R^2=0.85; Figure 1) followed closely by the familial richness of the Crustacea (R^2=0.81), while the goodness-of-fit for the familial richness of the Mollusca, Polychaeta and Echinodermata none-the-less indicated clear relationships (R^2= 0.62, 0.68, 0.57, respectively, Figure 1). The observed correlations appear to be independent of the richness and total abundance of each taxon, since the number of families identified over the entire study period for the Crustacea, Mollusca, Polychaeta and Echinodermata was 24, 32, 21 and 12 respectively and the number of individuals was 45 448, 21 636, 34 641 and 44 319 respectively.

The slope of the relationship between average surrogate familial richness and average total familial richness did not vary significantly with community age or deployment date (Table 1). In contrast, however, the goodness-of-fit of these relationships did depend on community age and/or deployment date for some surrogate taxa (Figure 2). While polychaetes showed a consistently good fit irrespective of community age, molluscs and echinoderms showed a linear decline in goodness-of-fit with increasing community age (molluscs: *slope* = -

0.67, *intercept*= 1.13, $P<0.0005$, $R^2=0.91$; echinoderms: *slope* = -0.09, *intercept*= 0.57, $P=0.005$, $R^2=0.59$). Thus, for these two phyla, the variability around the relationship depicted in Figure 1 increased as the community aged. The overall trend for the Crustacea and for the total abundance of all individuals appeared worse for communities of intermediate age, although there are too few data points to be certain of this trend.

5.4.2 Multivariate surrogates of community richness

5.4.2.1 Testing the robustness of SIMPER as a technique for selecting surrogate taxa

For each deployment date there was no consistent evidence of a directional decline in similarity with community age that could be linked to a temporal shift in the identity of the surrogate subset (Figure 3). However, for young communities < 5 months old there was some evidence of directional decline in similarity for the different deployment dates, suggesting a seasonal and/or successional influence in the identity of the surrogate subset (Figure 4). By corollary, families typical of a set of holdfasts are less influenced by the season of deployment when communities are allowed to develop for a longer time period. Not surprisingly, by selecting a larger number of families within the surrogate set (by changing the cut-off for including taxa), sensitivity to the season of deployment was usually reduced and, in most cases, low values of similarity between a given community and the reference point increased in magnitude (Figure 4).

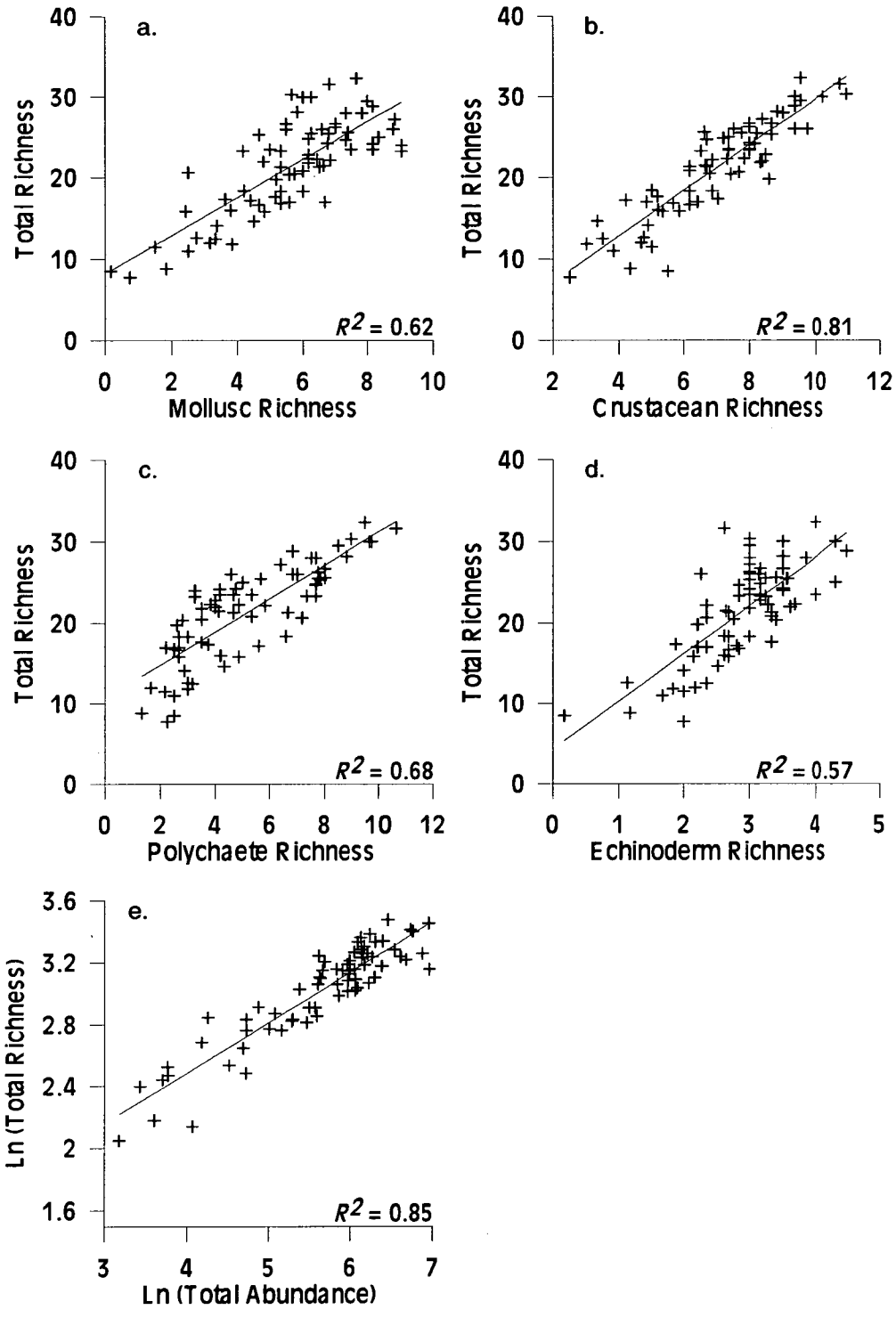


Figure 1 Relationship between mean number of taxa (mean total familial richness) and mean number of families in higher taxonomic groups (a-d) and mean total abundance (e). All means are based on 6 replicate holdfasts for each combination of deployment date * community age. (a) Molluscan richness, $y=2.35x + 8.22$; (b) crustacean richness, $y=2.81x+1.60$; (c) polychaete richness, $y=2.05x+10.72$; (d) echinoderm richness, $y=5.92x+4.40$; and (e) total abundance, $\ln(y)=0.33\ln(x)+1.18$. All regression analyses were significant at $P<0.0001$.

Table 1 ANCOVAs show that the slope of the relationship between average total richness and average richness of each higher taxa, and between average total richness and average total abundance, did not vary significantly with community age or date of deployment. Significant differences in these relationships among community ages or among dates of deployment would be indicated by a significant interaction ($P<0.05$) between the surrogate and community age/deployment date.

Test of surrogate*community age	*d.f.*	*F*	*P*
Mollusca	10, 47	1.93	0.07
Crustacea	10, 47	0.87	0.57
Polychaeta	10, 47	1.64	0.12
Echinodermata	10, 47	0.59	0.81
Ln(Total Abundance)	10, 47	0.59	0.81
Test of surrogate*deployment date	*d.f.*	*F*	*P*
Mollusca	10, 48	1.41	0.20
Crustacea	10, 48	1.17	0.33
Polychaeta	10, 48	0.74	0.69
Echinodermata	10, 48	1.07	0.40
Ln(Total Abundance)	10, 48	0.78	0.65

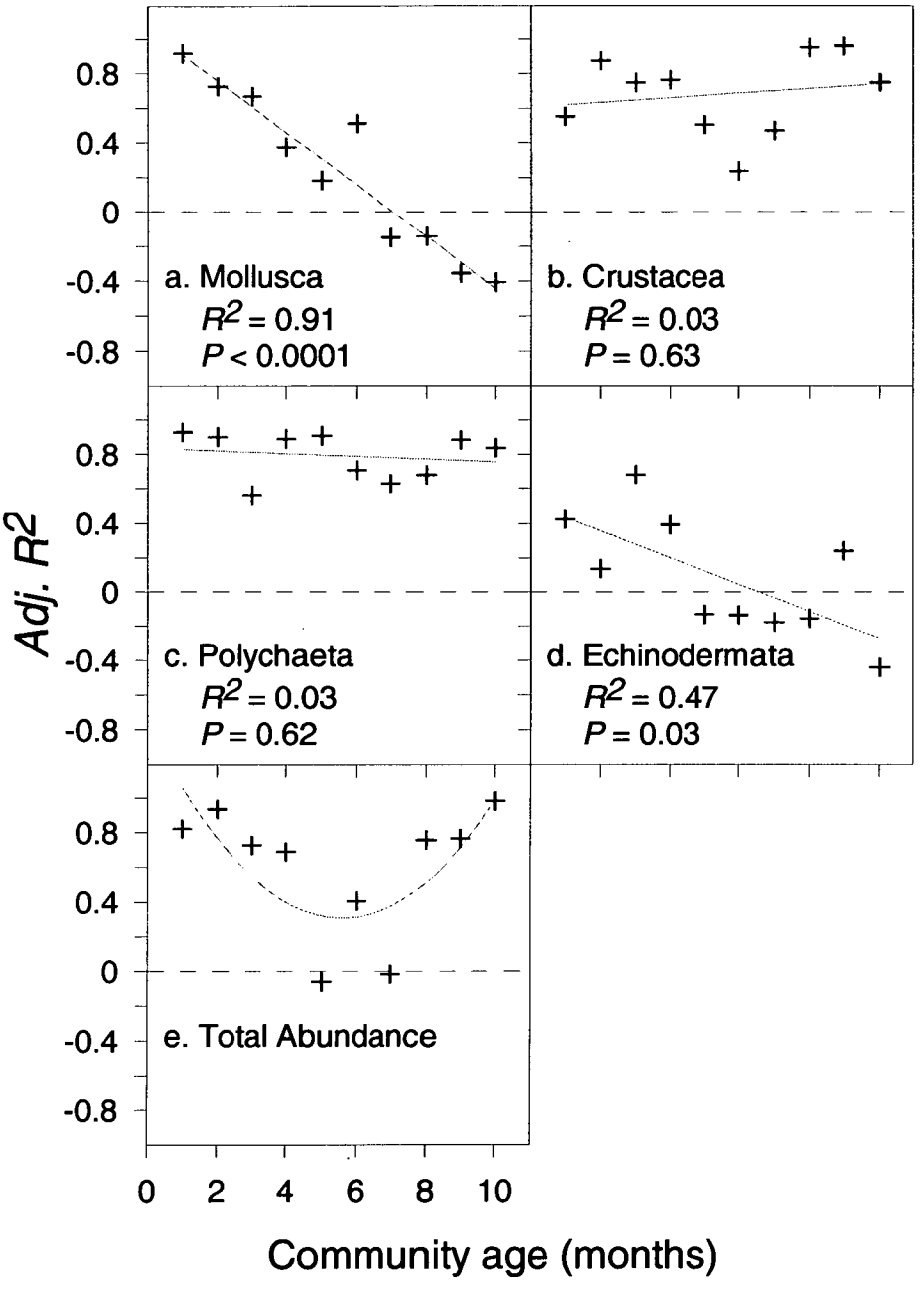


Figure 2 Change in the goodness-of-fit (*Adj R^2=adjusted R^2*) in the relationship between average number of taxa (average total familial richness) and the surrogate with age of the community. Surrogates are (a) molluscan familial richness, y=-0.15x+1.06; (b) crustacean familial richness, y=0.01x+0.61; (c) polychaete familial richness, y=-0.01x+0.84; (d) echinoderm familial richness, y=-0.08x+0.5; (e) and total abundance. Note that we used a regression technique able to calculate negative *Adj R^2* values (most statistical packages follow the convention of converting negative *Adj R^2* values to zero).

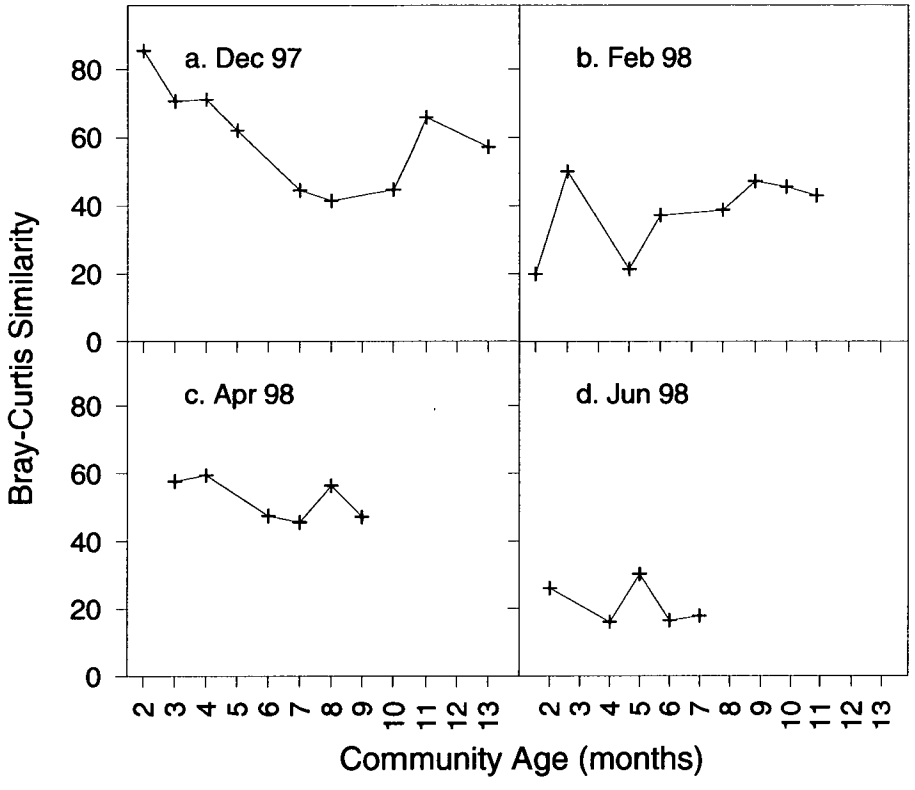


Figure 3 Bray-Curtis similarity between the surrogate set identified by SIMPER (PRIMER5) for each community age and the surrogate set identified by SIMPER for 1 month holdfasts, for several representative deployment dates (see Appendix 3 for all deployment dates). Taxa were included in a surrogate set if they contributed ≥5% to the total variation and had a ratio of mean to standard deviation ≥1.4. Deployment dates were (a) December 1997, (b) February 1998, (c) April 1998 and (d) June 1998.

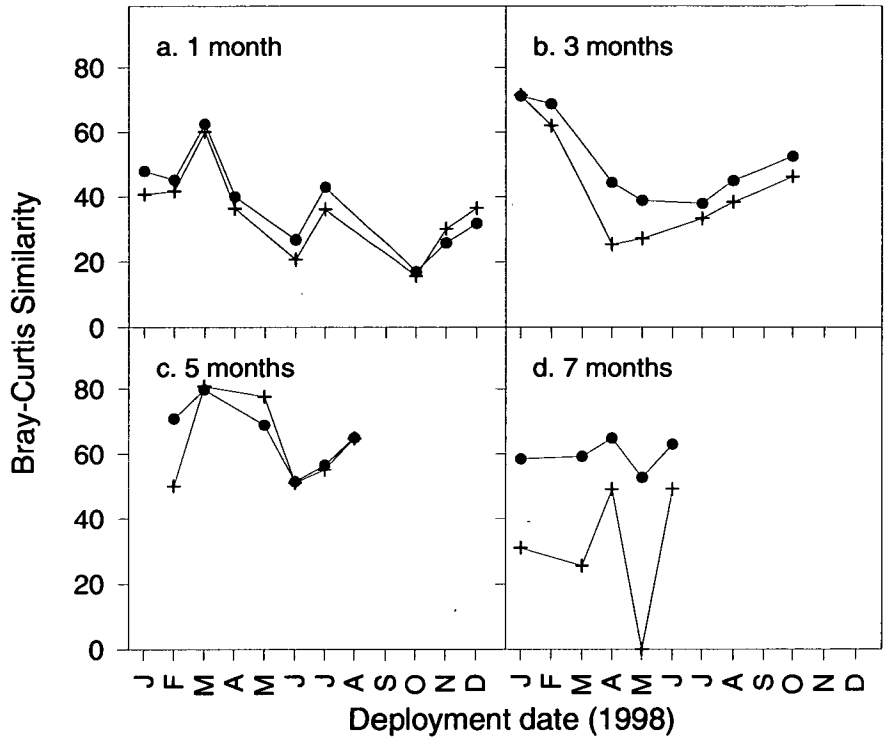


Figure 4 Bray-Curtis similarity between the surrogate set identified by SIMPER (PRIMER5) for each deployment date and the surrogate set identified by SIMPER for holdfasts deployed in December 1997, for several representative community ages (see Appendix 4 for all community ages). Two techniques were used to select surrogates: (+) taxa were included in a surrogate set if they contributed ≥5% to the average similarity within treatments and had a ratio of average similarity to standard deviation ≥1.4; and (•) taxa were included in a surrogate set in order of decreasing percent contribution to the average similarity within treatments until the cumulative contribution was 80% (note that this technique consistently selected a greater number of families in the surrogate set than the criteria based on contribution of ≥5% to average similarity). Community ages were (a) 1 month, (b) 3 months, (c) 5 months and (d) 7 months.

5.4.2.2 Comparison of multivariate surrogate communities

Predictably, the more families that occurred in a surrogate set the better the performance in matching the patterns evident in the complete data set containing all 100 families (Table 2). For a given number of families, BVSTEP tended to perform as well or better than a surrogate set selected on the basis of most abundant families, while SIMPER only did as well as selecting the most abundant families (Table 2). For a given number of families, both techniques were better than selecting families randomly, and there was no noticeable effect of the deployment date selected (Table 2). Basing surrogate sets on a single higher taxon did not improve performance over random selection of families, even when the number of families was high (*e.g.* 32 mollusc families identified; Table 2). Of the higher taxa examined, patterns among treatments based on Crustacea best reflected patterns indicated by the full suite of families, even though this group contained fewer families than the molluscs (Table 2).

Results based on all families suggest an interaction between deployment date and community age (Figure 5a). Older communities, particularly those ≥6 months, tend to cluster in a cloud. Younger communities (1 month) separate from this cloud, especially those developed in holdfasts deployed in cooler months. This suggests that succession towards a mature community occurs more quickly in the summer. This pattern becomes less clear as surrogate communities with progressively lower ρ_w values are selected, and is not readily discernable with a correlation less than $\rho_w = 87.05$ (Figures 5b-5f). By this criterion, this corresponds to identifying at least 10-15 families (*i.e.* 10-15% of

the total number of families detected). Results are presented for BVSTEP, however, using SIMPER to select surrogate sets, or simply basing the selection on the most abundant families, also produced similar results since ρ_w values of 91.33 and 90.54 were obtained for a selection of 14 families by SIMPER and a selection of 12 families on the basis of abundance, respectively (Table 2).

Table 2 Comparison of the similarity matrix contrasting communities defined by each combination of deployment date and community age based on all taxonomic groups (Bray-Curtis, fourth-root transformation) with the similarity matrix contrasting time intervals based on each surrogate set (Bray-Curtis, fourth-root transformation). Reference month (where applicable) refers to the deployment date used to select a surrogate set. Comparisons were made using the weighted Spearman rank correlation coefficient, ρ_w on the untransformed data, results are presented in descending order of goodness-of-fit (decreasing similarity).

Surrogacy technique	Reference month	Number of taxa in surrogate set	ρ_w
BVSTEP	March	20	95.32
BVSTEP	February	20	94.92
BVSTEP	January	20	94.19
most abundant families	n/a	20	93.92
BVSTEP	April	20	93.75
BVSTEP	February	15	93.16
BVSTEP	April	15	92.66
most abundant families	n/a	15	92.56
BVSTEP	January	15	92.38
SIMPER	March	14	92.26
SIMPER	April	13	92.12
BVSTEP	April	12	91.43
SIMPER	January	14	91.33
BVSTEP	January	10	90.90
BVSTEP	April	10	90.84
BVSTEP	February	10	90.74
BVSTEP	January	12	90.70
most abundant families	n/a	12	90.54
BVSTEP	March	15	90.37
BVSTEP	February	12	90.19
BVSTEP	March	12	89.40
most abundant families	n/a	10	89.20
Random selection	n/a	20	88.89
Crustacea only	n/a	24	88.02
BVSTEP	March	10	87.05
most abundant families	n/a	5	86.73
BVSTEP	April	5	86.64
SIMPER	February	6	86.18
Mollusca only	n/a	32	85.82
Polychaeta only	n/a	21	85.45
BVSTEP	January	5	85.31
BVSTEP	February	5	85.30
Random selection	n/a	20	84.10
Random selection	n/a	20	83.06
Random selection	n/a	20	82.19
Random selection	n/a	20	77.63
Echinodermata only	n/a	12	77.05
BVSTEP	March	5	76.41

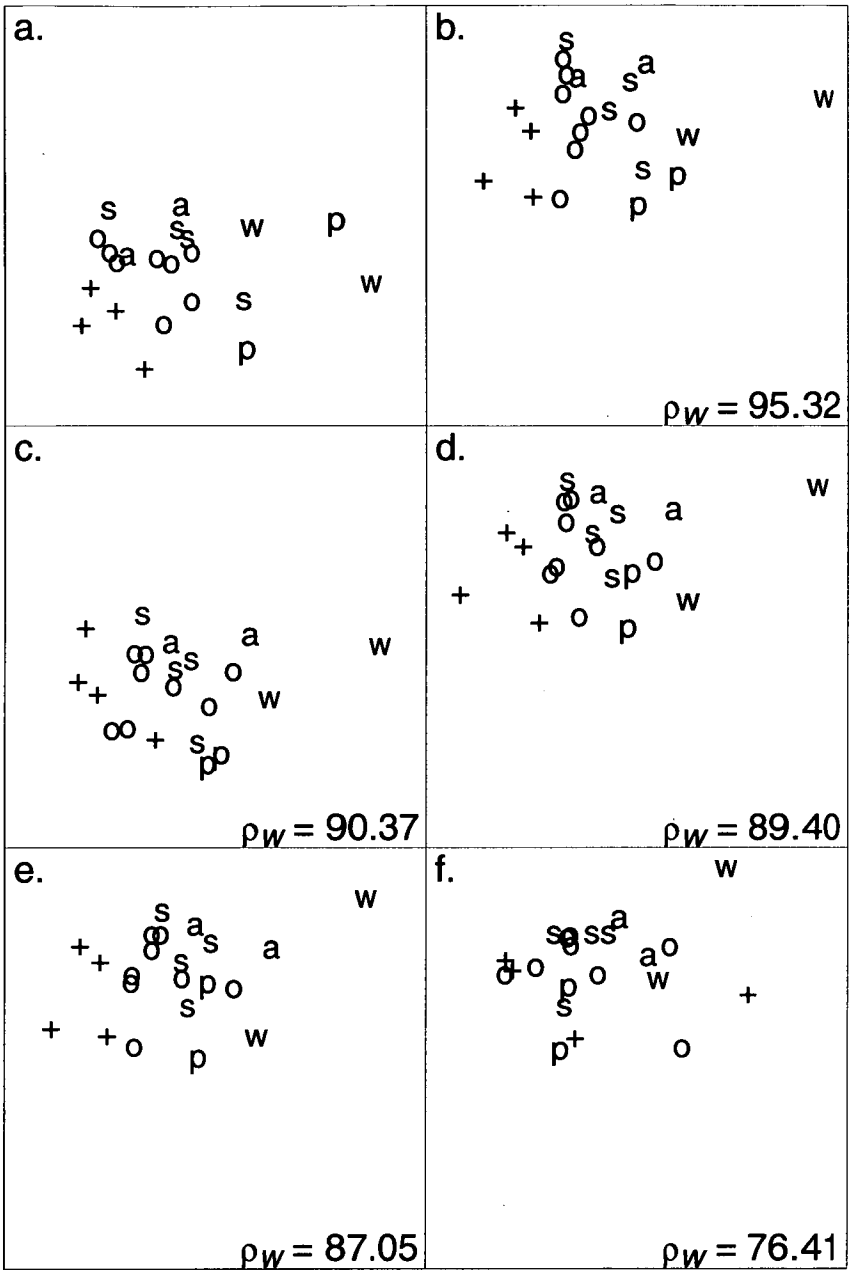


Figure 5 NMDS plots based on Bray-Curtis similarity (fourth-root transformed data) for (a) the full data set including all families; various surrogate sets selected using BVSTEP (data from the deployment date March 1998), based on selections of (b) 20 families, (c) 15 families, (d) 12 families, (e) 10 families, (f) 5 families. Bray-Curtis similarities were used to contrast all deployment dates and community ages, however, a subset of treatments are presented to assist interpretation; s = 1 month old communities deployed in December 1997, January 1998, February 1998 or December 1998, a = 1-month-old communities deployed in March or April 1998, w = 1-month-old communities deployed in June or July 1998, p = 1-month-old communities deployed in October or November 1998, o = all 3-month-old communities, + = all 10-month-old communities. ρ_w = weighted spearman rank correlation between the similarity matrix used to generate plot (a) and the similarity matrix used to generate each surrogate set (plots b-f).

5.5 Discussion

5.5.1 Univariate surrogates of community richness

Biodiversity is often presented as the total species (or familial) richness at a site or time (Fleishman et al. 2004). Because total richness itself can be difficult to measure, researchers have suggested the use of surrogates based on the richness of particular higher taxa (*e.g.* Pearson and Cassola 1992, Beccaloni and Gaston 1995, Gaston and Blackburn 1995, Garson et al. 2002, Lund and Rahbek 2002, Olsgard et al. 2003, Warman et al. 2004). While the familial richness of crustaceans, molluscs, polychaetes and echinoderms were all clearly correlated with total family richness in the artificial holdfasts, the best overall predictor of total richness was simply the total abundance of all individuals irrespective of taxonomic affinity. However, the correlation between a surrogate and total familial richness was not indicative of the temporal consistency in performance as a surrogate. The Polychaeta, which did not achieve the highest correlation with total familial richness, was the most consistent univariate surrogate of total familial richness across communities of a range of ages. The familial richness and total abundance of a given taxonomic group were not good predictors of its performance with respect to the overall correlation with total familial richness and the temporal consistency of this correlation. This was also true in the multivariate analysis. These observations raise the possibility that the variety of ecological and/or functional roles rather than the number of individuals or taxa within a taxon may be a better determinant of the suitability of a surrogate set. These results are similar to those of Anderson et al. (2005b), who also found high taxon richness was not highly correlated with a surrogate's ability to

predict biodiversity in macrofauna communities in natural kelp holdfasts across different spatial scales in north eastern New Zealand (although total abundance may have been).

5.5.2 Multivariate surrogates of family level community pattern

Since there are robust arguments to advocate use of multivariate similarity measures such as Bray-Curtis to compare biodiversity among sites (and times) rather than total species richness or Shannon-Wiener diversity (*e.g.* Cao et al. 1996, Su et al. 2004), we also tested the robustness of surrogates of multivariate patterns in community structure to temporal variation in community structure. Of the multivariate surrogate sets we examined, approaches that selected sets of taxa irrespective of their taxonomic affinities (*e.g.* Oliver and Beattie 1996, Fleishman et al. 2004), or which simply selected the most abundant taxa, performed consistently better than random selections of families, and selection of a single higher taxon, provided that a sufficient number of families were identified (>10% of all families). Our finding that using a single higher taxon as a surrogate of total biodiversity in marine communities is sub-optimal, is consistent with the results of Anderson et al. (2005b) but not of some others. In contrast with our conclusions, Gladstone (2002) suggested that marine reserves established to conserve mollusc diversity would also adequately protect total biodiversity (of non-cryptic animals >5 mm maximum dimension) on rocky shores in New South Wales, Australia, while Olsgard and Somerfield (2000) and Olsgard et al. (2003) showed that polychaetes are suitable surrogates of biodiversity in soft-sediment communities. These contrasting results probably reflect differences in the ecological roles of these higher taxa in different habitat

types and highlight the importance of validating a surrogacy technique for the specific community being examined. We note however, that none of the above authors examined the performance of their surrogates across time intervals of different magnitude or season, nor did they compare the performance of their selected surrogates to other selections of taxa where taxonomic affinity was ignored.

5.5.3 How should surrogates be identified?

While the specific taxa selected as a surrogate suite will vary among different communities and possibly even among similar communities in different environments, the techniques used to select taxa apply to any community type. Among the several techniques for selecting surrogate sets that did perform well, the choice of which to use will largely depend on the nature of the reference data used to select surrogates. Techniques that require information to compare between treatments (in our case, the different combinations of deployment date and community age) such as BVSTEP (Clarke and Warwick 2001) appear to be most useful. Under these circumstances, the surrogate is selected because it correlates best with the change in overall community structure it is intended to detect. However, this approach requires access to pilot data collected across several treatments or through time.

Where these kinds of pilot data are not available (for example, because of the expense of obtaining data), techniques that select taxa because they are abundant and consistent can also be used (*e.g.* BVSTEP, SIMPER or the selection of abundant taxa). However, in this case, selection of surrogates should be

confirmed subsequently since the composition of the surrogate set may vary with time. Encouragingly, our results showed that, for macrofauna communities of kelp holdfasts, similar surrogate communities were identified (with SIMPER) for holdfast communities deployed on different dates and for different community ages, as long as a sufficient number of taxa were identified (ca. 10% of the total) and the community was not at a very early stage of succession, particularly for deployments in winter months. Note that the performance of SIMPER was similar to that of using the most abundant families; however, we used SIMPER to select families that were both abundant and also consistently present in time. On this basis, using SIMPER to select surrogates should be preferred over selection of taxa based only on abundance.

5.5.4 Conclusions

Our results show that temporally robust surrogates can be identified. However, the nature of these surrogates will depend on how biodiversity is defined (Noss 1990), the type of community under study and whether baseline data are available across several consecutive sampling periods or from only a single sampling. Regardless of which surrogate is selected for study, the spatial and temporal robustness of the surrogate should be examined across relevant scales of observation. Where temporal data are not available, information on temporal variation might be gained by examining spatial variation in cases where the disturbance history of patches or lineal geographic features (*e.g.* coastlines) is known. Patches on a benthic 'landscape' may be on an attractor describing oscillating community dynamics but out of phase (Habeeb et al. 2005).

We note that the capacity to identify surrogates of kelp holdfast macrofauna communities that are temporally stable over 13 months does not mean that the surrogates will continue to be stable over longer time periods. Similarly, the effectiveness of a surrogate may differ before and after environmental impact. Environmental impact that disrupts community structure may change the relationship between a taxon and total biodiversity (*e.g.* Smith 1996a, Olsgard and Somerfield 2000). Regular validation of a surrogate's performance is required throughout any monitoring program, particularly in the face of changing patterns of disturbance.

6 GENERAL DISCUSSION

6.1 Introduction

A key question in ecology is whether communities are real units of biological organisation with emergent properties subject to selection. The issue is important not just at an abstract academic level but because the approach used to manage or study these communities will depend on how they are organized (Simberloff 2004). Because we cannot understand community dynamics without knowledge of the processes underpinning community development (Drake 1990, Samuels and Drake 1997, Cadotte et al. 2005), a sensible first step in addressing this question for any community is to describe the assembly process. For example, the history of assembly may influence the ongoing community dynamics of a system by leading to different interaction intransitivities (Drake 1991). A community that displays a broadly consistent assembly pattern regardless of the order of the arrival and abundance of taxa, and thus whose structure reflects predictable post-settlement processes and not merely the accumulation of settlers, is likely to be a real community rather than a haphazard collection of species adapted to similar physical conditions (Underwood 1986). The major aim of this thesis was to examine the processes involved in the assembly of kelp holdfast communities; a secondary aim was to assess how the process of assembly fits with current models of community succession. In addition, the study provided an opportunity to test hypotheses generated from studying sessile marine communities, using a community dominated by mobile species, and to assess the suitability of these communities as models for environmental impact assessment and for testing general principles in ecology.

6.2 Community assembly in holdfast macrofauna communities

Various models of succession in communities have been proposed, including Clements' (1916) entirely deterministic view, and the three models of Connell and Slayter (1977).

6.2.1 Macrofauna community assembly is not 'Clementsian'

In a Clementsian assembly, the identity of early colonizers are the same regardless of timing and location. This was the predominate view on community development for a number of years (Connell and Slayter 1977), but is not widely accepted today and is not supported by this study. If viewed after 5-6 months of assembly, the holdfast communities examined here did appear to be broadly similar in community structure, in line with a Clementsian view (Chapter 2). However, the assembly process was not deterministic because the identity of early colonisers was highly variable throughout the study (Chapter 4), and the season of deployment strongly influenced the rate of community development (Chapter 2). Similar results have been obtained in other macrofauna communities associated with artificial habitats in New South Wales, Australia (Underwood and Chapman 2006), which suggests that this pattern may be more broadly applicable to other types of macrofauna communities. The convergence of community structure occurred within 5 months of deployment (depending on season; Chapter 2), in line with estimates of the development of similar communities elsewhere (Costello and Myers 1996, Gee and Warwick 1996, Underwood and Chapman 2006).

6.2.2 Macrofauna community assembly does not fit with other traditional models of succession

Connell and Slayter (1977) outlined 3 basic models of succession in sessile communities, *viz.* facilitation, tolerance and inhibition. The common ground between all three is that early colonising species can influence the ability of later species to colonise by altering the environment post-colonisation (*e.g.* by consuming resources or by modifying physical habitat), and early colonisers are eventually replaced by these later colonising species. For at least two reasons, community assembly in holdfast communities did not fit clearly with any single model. First, there was evidence of both positive (facilitative) and negative (inhibitive) interactions within a single community (Chapters 3 and 4), and second, there was little evidence of replacement of families during the assembly process (Chapter 3).

There is some divergence in results from different studies on the role of species replacements in macrofauna communities. Community development in macrofauna communities is generally thought to occur via accumulation rather than replacement (*e.g.* Ojeda and Santelices 1984, Dean and Connell 1987a, Edgar 1991a, Smith et al. 1996). Using a similar design to that employed here, Underwood and Chapman (2006) found that assembly of macrofauna communities associated with artificial habitats (pot scourers) in New South Wales, did appear to include replacements. A possible mechanism for species replacement in macrofauna communities is that highly mobile species may be more likely to arrive in a new habitat first, but ultimately they become excluded through the increased occupation of space by sessile species (Costello and

Myers 1996). Underwood and Chapman (2006) observed that the standardized multivariate community structure of their communities varied significantly as they developed, indicating that the taxonomic composition of their communities changed through development. They concluded that this must be a result of replacements because overall richness did not vary significantly as their communities aged. It is difficult to compare the different studies because of differences in experimental design, location, community composition, timing of deployment, length of deployment period and taxonomic resolution; it may simply be that the dynamics of macrofauna communities vary with all of these factors. However, it is also possible that the results of Underwood and Chapman (2006) may have been driven by differences in the power between the multivariate test used to look for changes in community composition, and the univariate test used to test for differences in richness.

6.2.3 Pre-emption of space was important but not complete

Space pre-emption, observed commonly in artificial habitats containing sessile species, may also influence the dynamics of other macrofauna communities (*e.g.* Costello and Myers 1996, Smith and Rule 2002). Inhibition of settlement is clearly important in holdfast macrofauna community assembly because the richness of older actual communities (≥3 months) was notably less than that expected based on accumulation of monthly recruitment (Chapters 3 and 4). Importantly, the cause of this difference was not the post-recruitment interactions among established individuals in the community, because incorporating mortality and emigration did not improve the fit of model communities to predicted communities (Chapter 4). However, the pre-emption

was not absolute since a number of recruits were able to gain a foothold in established communities each month, significantly influencing both community structure and community variability (Chapter 4).

6.3 The mechanisms underpinning succession

Describing succession or assembly requires more than just a description of pattern; information is also required on the mechanisms that generate pattern (Farrell 1991). A 'real' community is more likely to occur when community structure and dynamics are more influenced by internal processes, such as species interactions, than external processes, such as the supply of recruits and weather.

The convergence in community structure observed in Chapter 2 is most parsimoniously explained by an increase in the relative importance of species interactions over the supply of new individuals as the community aged (Chapter 3). These interactions appeared to be most important between the established community and potential recruits (Chapter 4). Interactions were predominately negative (i.e. inhibition of settlement, or pre- or post-settlement predation, or post-settlement but pre-recruitment competition) but there was also evidence of facilitation in at least two families (Chapter 3 and 4).

The outcome of particular species interactions would also need to be largely consistent in space and time to lead to convergence in community structure during assembly. Analysis of the net effect of all inter- and intra-specific interactions suggested that this is likely to be the case (Chapter 4). This observation is also consistent with the surrogacy analysis outlined in Chapter 5.

In a changing community the mechanism for a consistent relationship between a surrogate and the entire community is likely to be a consistent set of interactions. More detailed experimentation is required to be certain, since interaction topologies can be complex in a species-rich community (Johnson and Seinen 2002).

6.4 Conclusions

6.4.1 Community dynamics of mobile vs. sessile marine communities

Much of the theory on the dynamics of temperate marine invertebrate communities is based on the dynamics of populations and communities of sessile, particularly intertidal, species (Menge and Branch 2001). In these communities the ability for movement is limited largely to larval stages (the exception being fragmentation). The dynamics of these communities may be very different to other marine communities where adults may be highly mobile (Frid 1989). The capacity for movement may have implications for the effects of competition and predation and on life-history strategy.

In this study, the recruitment of adults and juveniles were grouped as a single entity and so their relative importance could not be determined. However, it was possible to determine whether the role of recruitment was similar in a mobile community compared with sessile communities. Our results on the relative role of recruitment versus species interactions are similar to those from studies of sessile communities (*e.g.* Gaines and Roughgarden 1985, Connolly and Roughgarden 1999b, Connolly et al. 2001), with the notable exception that, in

holdfast communities, recruitment continued to significantly influence community structure and variability throughout community development despite a lack of disturbance. The mechanism for a continuous and ongoing role of recruitment was linked to decreases in abundance through emigration and/or mortality (Chapter 4). Emigration, in particular, can be very high in macrofauna communities (Costello and Myers 1996, Norderhaug et al. 2002, Jorgenson and Christie 2003, Waage-Nielsen et al. 2003; but see also Thiel and Vásquez 2000). Smith (2000) also described the ongoing influence of recruitment on the community structure of established macrofauna communities associated with *Ecklonia radiata* in New South Wales. Through this indirect pathway, variability in recruitment can impact on community variability at small spatial scales. High, small-scale variability is a commonly observed phenomenon in marine benthic systems (*e.g.* Lively et al. 1993, Underwood 1996, Dunstan and Johnson 1998, Benedetti-Cecchi 2001, Coleman et al. 2002, Anderson et al. 2005a, Fraschetti et al. 2005).

6.4.2 Are holdfast communities real?

While Underwood (1986) was skeptical about the usefulness of differentiating between communities and assemblages, he described two features that were more likely to be characteristic of real communities than assemblages. First, real communities are likely to converge in structure during assembly; and, second, this convergence should result in a community structure that shows persistence stability (note that persistence need not necessarily infer equilibrium; Grover and Lawton 1993). Furthermore, these properties should hold through space and time (Underwood 1986). Communities associated with *E. radiata* holdfasts have been shown to be broadly consistent across large spatial scales in New Zealand

(Anderson et al. 2005a, Anderson et al. 2005b), although Rule and Smith (2005) in New South Wales found that results could be variable among different taxonomic groups. In this study there were clear signs of convergence in community structure (Chapter 2) even though recruitment varied across the different deployment dates (Chapter 4). At a finer scale of resolution, the structure of the converged community was variable (Chapter 2), which was partly explained by variability in recruitment (Chapter 4), over a time scale likely to be sufficient to see turnover of most taxa. Thus, by the criteria suggested by Underwood (1986) these communities do appear to be more than just assemblages.

Wilson (1997) discussed the possibility that some communities may be functionally organised to the extent that selection could occur at levels higher than the individual. Community level selection is more likely to occur in real communities (rather than assemblages) where individuals have a greater potential to affect local community composition as a unit (the concept of 'shared fate'; Wilson 1997). Shared fate can readily arise in circumstances where spatial self-organising occurs in communities (Johnson and Boerlijst 2002). Whether holdfast communities are functionally organized in this sense was not tested. Wilson (1997) proposed that community level selection could occur in communities that are self-contained and which display differences in reproduction and survival. Because kelp holdfast communities do appear to be real communities, and 100s of communities can exist on a single landscape (and thus the potential for differences in community level fitness exists), this type of community may be a useful model for examining this question.

The findings of this study have important implications for the way in which experiments are conducted with macrofauna communities, particularly when microcosms or artificial habitats are used to describe the dynamics of a naturally occurring community. The interactions that occur within these communities have a large effect on the structure and dynamics observed. Since the physical structure of a habitat can influence the nature of species interactions (Warfe and Barmuta 2006), it will often be important that the structure of an artificial habitat is similar to a naturally occurring community. Because species interactions are important, it is also likely that co-evolutionary processes are involved in community development, which means that communities constructed from subsets of a larger community, or which are based on laboratory reared cultures (*e.g.* Drake 1991), may not display dynamics representative of natural communities.

6.4.3 The use of kelp holdfasts as 'model' communities

Anderson et al. (2005b) and Smith (2000) have suggested that kelp holdfast may make good models for the detection of environmental impacts because of their consistency in structure and sensitivity to anthropogenic impacts, but that more information is required on their temporal consistency (see also Rule and Smith 2005). Our results show that these communities can also be temporally consistent and that suitable surrogates can be used to reduce issues associated with their high diversity and incomplete taxonomy (Chapter 5). Thus, these communities may be useful models, not just for examining environmental impacts but also for studying more general questions in community ecology.

Such tools are necessary to bridge the gap between the observational studies of large-scale, species-rich communities and manipulative experiments based on mathematical models or species-poor microcosms. Some caution is required if artificial holdfasts are used to estimate recruitment, if the aim is to mimic recruitment to a real community, but their use in concert with naturally occurring holdfasts communities should create a valuable tool for resolving some of the many questions still unanswered in ecology.

7 APPENDICES

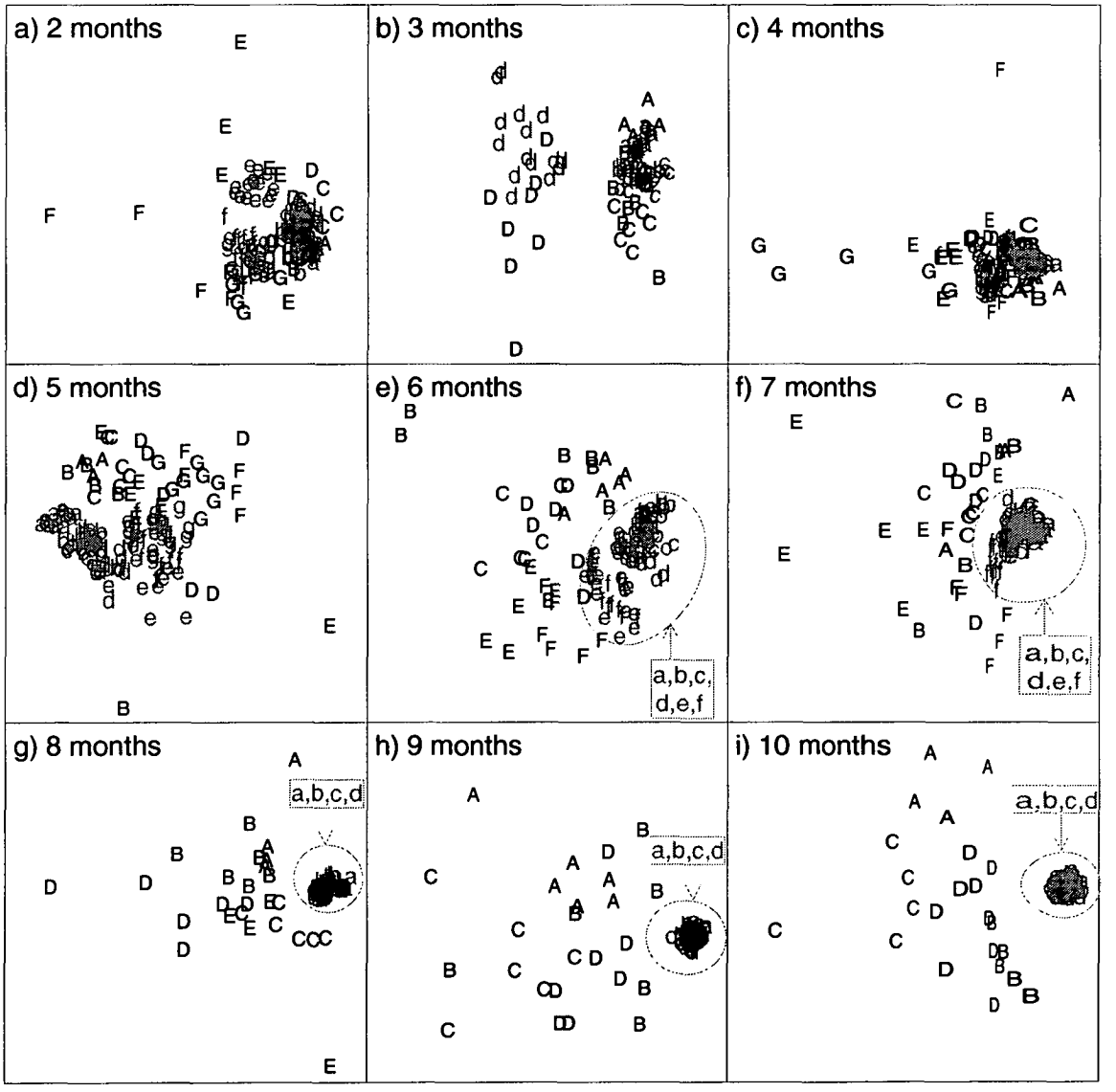
Appendix 1 List of taxa identified, family codes used and identification numbers from the Code for Australian Biota (CAAB code; Rees et al. 1999-).

Family code	Phylum	Family or alternative classification	CAAB Code
76	Cnidaria	Undifferentiated Order Actinaria	11 229000
14	Platyhelminthes	Other undifferentiated Turbellaria	13 010000
23	Platyhelminthes	Unidentfied Class Turbellaria A	13 010000
100	Nematoda	Undifferentiated Phylum Nematoda	16 000000
99	Sipuncula	Undiffferentiated Phylum Sipuncula	17 000000
24	Annelida	Family Eunicidae	22 024000
30	Annelida	Family Flabelligeridae	22 116000
27	Annelida	Family Oenonidae	22 029000
26	Annelida	Family Nereididae	22 056000
16	Annelida	Family Pholoididae	22 058000
15	Annelida	Family Phyllodocidae	22 059000
34	Annelida	Family Sabellidae	22 083000
36	Annelida	Family Spirorbidae	22 000000
33	Annelida	Family Serpulidae	22 085000
32	Annelida	Family Terebellidae	22 120000
17	Annelida	Unidentified errant Class Polychaeta A	22 000000
18	Annelida	Unidentified errant Class Polychaeta B	22 000000
19	Annelida	Unidentified errant Class Polychaeta C	22 000000
20	Annelida	Unidentified errant Class Polychaeta D	22 000000
21	Annelida	Unidentified errant Class Polychaeta E	22 000000
22	Annelida	Unidentified errant Class Polychaeta F	22 000000
25	Annelida	Unidentified errant Class Polychaeta G	22 000000
28	Annelida	Unidentified errant Class Polychaeta H	22 000000
29	Annelida	Unidentified errant Class Polychaeta I	22 000000
31	Annelida	Other undifferentiated errant Class Polychaeta	22 000000
35	Annelida	Other undifferentiated sedentary Class Polychaeta	22 000000
61	Mollusca	Family Nassariidae	24 000000
50	Mollusca	Family Lottiidae	24 010000
49	Mollusca	Family Fissurellidae	24 040000
51	Mollusca	Family Trochidae	24 046000
63	Mollusca	Family Cerithiidae	24 076000
67	Mollusca	Family Litiopidae	24 078000
58	Mollusca	Family Turritellidae	24 079000
57	Mollusca	Family Vanikoridae	24 131000
59	Mollusca	Family Ranellidae	24 176000

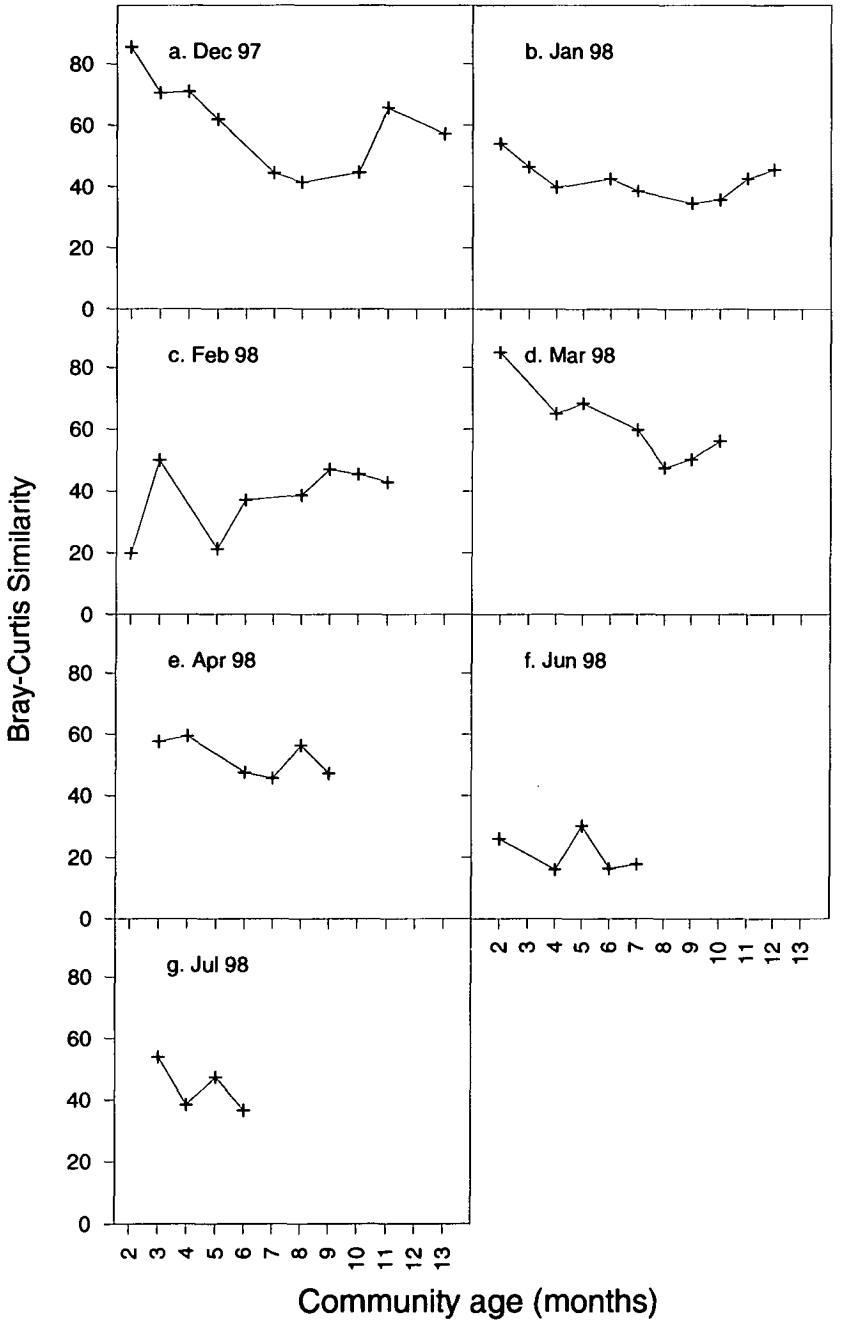
Family code	Phylum	Family or alternative classification	CAAB Code
68	Mollusca	Family Tonnidae	24 177000
64	Mollusca	Family Epitoniidae	24 191000
60	Mollusca	Family Columbellidae	24 203000
43	Mollusca	Family Marginellidae	24 210000
66	Mollusca	Family Costellariidae	24 213000
40	Mollusca	Unidentified Order Nudibranchia	24 420000
39	Mollusca	Family Philinidae	24 322000
62	Mollusca	Unidentified Class Gastropoda A	24 000000
65	Mollusca	Other Undifferentiated Class Gastropoda	24 000000
44	Mollusca	Family Mytilidae	23 220000
45	Mollusca	Family Pteriidae	23 236000
54	Mollusca	Family Ostreidae	23 257000
47	Mollusca	Family Pectinidae	23 270000
56	Mollusca	Family Carditidae	23 325000
55	Mollusca	Family Cardiidae	23 335000
48	Mollusca	Family Veneridae	23 380000
46	Mollusca	Family Hiatellidae	23 395000
53	Mollusca	Unidentified Class Bivalvia A	23 199000
52	Mollusca	Unidentified Class Bivalvia B	23 199000
42	Mollusca	Family Octopodidae	23 659000
37	Mollusca	Family Chitonidae	23 118000
38	Mollusca	Unidentified Phylum Mollusca A	23 000000
41	Mollusca	Unidentified Order Teuthoidea A	23 615000
75	Arthropoda	Undifferentiated Class Ostracoda	27 100000
83	Arthropoda	Unidentifed Order Leptostraca A	28 000000
82	Arthropoda	Undifferentiated Order Mysidacea	28 079000
1	Arthropoda	Undifferentiated Class Pycnogonida	33 017000
88	Arthropoda	Undifferentiated Order Tanaidacea - Apseudomorph	28 105000
84	Arthropoda	Undifferentiated Order Tanaidacea - Tanaidomorph	28 105000
79	Arthropoda	Family Anthuridae	28 205000
92	Arthropoda	Family Arcturididae	28 278000
86	Arthropoda	Family Gnathiidae	28 202000
78	Arthropoda	Family Idoteidae	28 284000
80	Arthropoda	Family Janiridae	28 324000
81	Arthropoda	Family Podoceridae	28 548000
89	Arthropoda	Family Serolidae	28 225000
77	Arthropoda	Family Sphaeromatidae	28 226000
87	Arthropoda	Unidentified Order Isopoda A	28 200000

Family code	Phylum	Family or alternative classification	CAAB Code
93	Arthropoda	Family Caprellidae	28 594000
94	Arthropoda	Undifferentiated Sub Order Gammaridea	28 400000
90	Arthropoda	Family Palinuridae	28 820000
91	Arthropoda	Undifferentiated Caridea	28 710000
70	Arthropoda	Family Paguridae	28 835000
74	Arthropoda	Unidentified Order Decapoda G (crab)	28 708000
71	Arthropoda	Family Majidae	28 880000
69	Arthropoda	Family Hymenosomatidae	28 885000
73	Arthropoda	Family Cancridae	28 904000
72	Arthropoda	Unidentified Order Decapoda F (crab)	28 708000
85	Arthropoda	Unidentified Phylum Crustacea A	27 000000
7	Echinodermata	Family Antedonidae	25 060000
8	Echinodermata	Unidentified Class Crinoidea B	25 001000
4	Echinodermata	Family Ophiotrichidae	25 192000
5	Echinodermata	Unidentified Class Ophiuroidea A	25 160000
6	Echinodermata	Unidentified Class Ophiuroidea B	25 160000
2	Echinodermata	Family Cucumariidae	25 408000
3	Echinodermata	Other undifferentiated Class Holothuroidea	25 400000
10	Echinodermata	Family Asterinidae	25 140000
9	Echinodermata	Family Asteriidae	25 154000
11	Echinodermata	Unidentified Class Asteroidea A	25 102000
13	Echinodermata	Family Echinometridae	25 247000
12	Echinodermata	Unidentified Class Echinoidea A	25 200000
95	Chordata	Family Gobiesocidae	37 206000
96	Chordata	Family Scorpaenidae	37 287900
98	Chordata	Family Clinidae	37 416000
97	Chordata	Unidentified Infraclass Teleostei A	37 000000

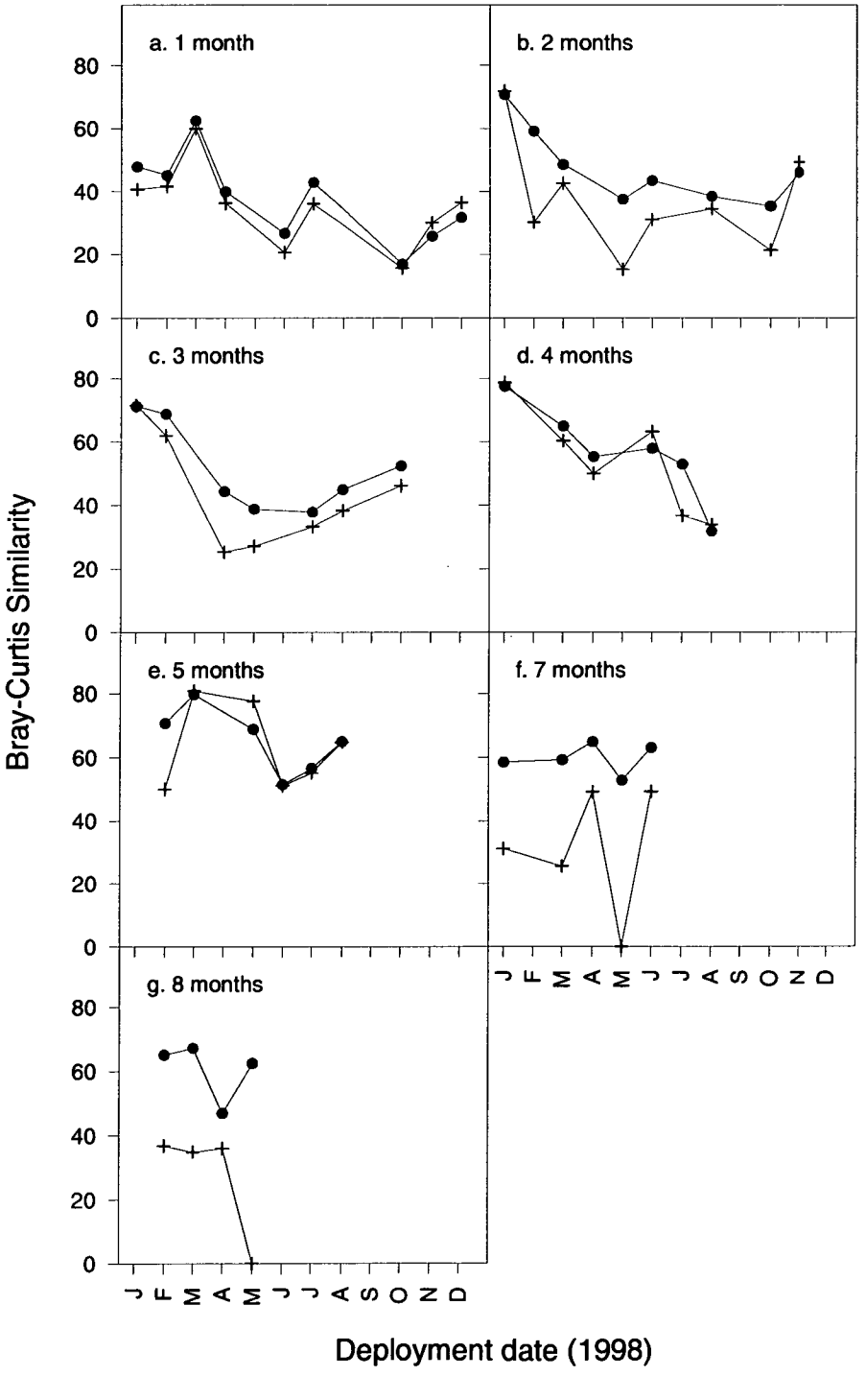
Appendix 2 NMDS plots based on Bray-Curtis similarities (fourth-root transformed data) among actual holdfast communities (A-F) and predicted communities (a-f) based on accumulated recruitment of 1-month time intervals, for the same community age. This analysis is based on raw abundances but shows similar pattern to that based on analysis of standardised data (see Figure 2). For a given nMDS plot matching upper and lower case letters have the same deployment date and the sequence of letters represents the temporal sequence in deployment dates. Community ages were (a) 2 months (stress=0.17), (b) 3 months (stress=0.14), (c) 4 months (stress=0.17), (d) 5 months (stress=0.20), (e) 6 months (stress=0.17), (f) 7 months (stress=0.16), (g) 8 months (stress=0.11), (h) 9 months (stress=0.11) and (i) 10 months (stress=0.10).



Appendix 3 Bray-Curtis similarity between the surrogate set identified by SIMPER (PRIMER5) for each community age and the surrogate set identified by SIMPER for 1 month holdfasts, for each deployment date. Taxa were included in a surrogate set if they contributed ≥ 5% to the total variation and had a ratio of mean to standard deviation ≥ 1.4. Deployment dates were (a) December 1997, (b) January 1998, (c) February 1998, (d) March 1998, (e) April 1998, (f) June 1998 and (g) July 1998.



Appendix 4 Bray-Curtis similarity between the surrogate set identified by SIMPER (PRIMER5) for each deployment date and the surrogate set identified by SIMPER for holdfasts deployed in December 1997, for each community age. Two techniques were used to select surrogates: (+) taxa were included in a surrogate set if they contributed ≥ 5% to the average similarity within treatments and had a ratio of average similarity to standard deviation ≥ 1.4; and (solid circles) taxa were included in a surrogate set in order of decreasing percent contribution to the average similarity within treatments until the cumulative contribution was 80% (note that this technique consistently selected a greater number of families in the surrogate set than the criteria based on contribution of ≥ 5% to average similarity). Community ages were (a) 1 month, (b) 2 months, (c) 3 months, (d) 4 months, (e) 5 months, (f) 7 months and (g) 8 months.



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